GENETICS IN PLANT AND ANIMAL IMPROVEMENT

DONALD FORSHA JONES

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GENETICS IN PLANT AND ANIMAL IMPROVEMENT

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BY

DONALD FORSHA JONES

CONNECTICUT AGRICULTURAL EXPERIMENT STATION
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TO

Edward Murray East

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PREFACE

THE following pages have grown out of a course of lectures given at the University of Arizona and at Syracuse University, modified by the experience of applying theories developed in the laboratory to the needs of the farm. The desirability of presenting the subject in the simplest form to the beginning student and to the general reader has made it impossible to include much of the important work which has been done in advancing the science of Genetics. In selecting the experimental results that are used to illustrate the fundamental principles, the author does not hope to have made the best choice in every case. Naturally, the investigations carried on at the Connecticut Experiment Station have been drawn upon freely on account of their greater familiarity.

The book is designed primarily as a text-book for the first course in Genetics. Where this is followed in agricultural colleges by applied courses in Plant and Animal Breeding, the last two chapters are designed to be supplemented by such books as Winters' "Animal Breeding" and Hayes and Garber's "Breeding Crop Plants." These two chapters are needed to make the book more complete for the general reader and for the student who may not have an opportunity to continue the subject, yet may wish to have some knowledge of the methods of plant and animal improvement now in practice. Whether or not the reader is intimately concerned with the business of plant and animal production, he can readily appreciate the need for the close association between theory and practice, which has been made throughout the book.

In preparing the manuscript, free use has been made of other books, particularly Walter's "Genetics," Babcock and Clausens' "Genetics in Relation to Agriculture," and East and Jones' "Inbreeding and Outbreeding." The very great help given by Dr. E. H. Jenkins in revising the manuscript, and the valued suggestions and criticisms as to the arrangement and presentation of the subject matter, made by Dr. L. C. Dunn and Dr. E. W. Sinnott, are gratefully acknowledged. Several chapters have been read and commented upon by Dr. L. J. Cole, Mr. E. N. Wentworth, and Dr. E. M. East. Mr. P. C. Mangelsdorf has given needed help in reading the proofs. The author also wishes to record his appreciation for permission to reproduce illustrations and tabular material from many sources. In every case credit is given for borrowed material by citing the name of the author and the place of original publication as far as known. Special thanks are due Mr. R. C. Cook, Editor of the *Journal of Heredity*, for making available many of the illustrations.

D. F. Jones.

New Haven, Conn.
November 24, 1924.

GENETICS IN PLANT AND ANIMAL IMPROVEMENT

CHAPTER I

INTRODUCTION

GENETICS AND ITS APPLICATION TO AGRICULTURE

To meet the ever-growing need of the world for food and clothing by increased plant and animal production, two general methods are available: one is by bettering the conditions in which plants and animals are grown; the other is by increasing their inherent productive capacity. The first is brought about by better husbandry through the application of improved methods of culture, such as more intensive tillage and fertilization, more economical utilization of food by animals, and more effective ways of controlling insects and diseases. The second necessitates an increased ability on the part of economic animals and plants to grow and to produce.

Possibilities of increased production.—Before considering the nature and use of genetics in the service of agriculture, let us briefly notice some possibilities of the first method, good husbandry. The bringing into cultivation of vast areas of untouched soil, which has so largely contributed to our abundant supplies of food and clothing in the past, is no longer possible. No new continents await the explorer. It is true that large tracts of what is now waste land will be made productive, but only when the

increased market value of the crops that can be grown upon them justifies the expense of reclamation. In spite of the fact that increased production does not always return the greatest profit to the producer, it is fundamentally necessary to use all means of increasing the products from the soil as long as they can be produced profitably. So much is yet to be accomplished by proper attention to the cultural factors that the first emphasis rightly belongs there. Still further, production can be increased by utilizing animals and plants which are as yet undomesticated but which may have value.

Importance of plant and animal introductions.—The organized search of the Office of Foreign Seed and Plant Introduction of the United States Department of Agriculture has proved that many plants exist in the far corners of the earth, both in the wild and under cultivation, which can be used to some advantage. With the exception of corn, cotton, potatoes, and tobacco, nearly all of our staple crops were brought to this country by the early settlers. In more recent times, the navel orange from Brazil, varieties of the date palm from Africa and Mesopotamia, the fig from Asia Minor, the soy and velvet beans from Japan and China, and long-staple cotton from Egypt, have been introduced and have added considerably to our prosperity.

Valuable plants which are unknown or unappreciated exist even in our own country. A good illustration of this is found in the tepary bean. Long before the coming of Columbus, the original inhabitants of the arid Southwest practiced an extensive agriculture. The conditions of extreme heat and a short rainy season of six weeks or two months during the middle of the summer forced them to develop crops especially fitted to these surroundings. Not until recently was it recognized that the beans raised many centuries ago by the Indians occupying those regions, and still cultivated by their descendants, differ radically from the commonly cultivated varieties of this plant. In fact, this form has been classified as a new botanical species

(*Phaseolus acutifolius*) and has been found to withstand conditions of heat and drought under which ordinary beans (*Phaseolus vulgaris*) produce little or nothing. In the same surroundings, the tepary is remarkably productive. While

FIG. 1.—The citrus fruits, brought to this country by the Spaniards, are now grown on many thousands of acres. The Washington navel orange introduced from Brazil by the U. S. Dept. of Agriculture is a valuable addition to the list of varieties grown in California. (Courtesy of La Hacienda.)

it lacks something in quality, it has been found to be a valuable plant for large areas of the Southwest. The sunflower is now being used for ensilage and is another example of a native species with long-unappreciated possibilities.

Sweet clover, once a roadside weed, is now an important forage and green-manure crop.

While a few of the plant and animal immigrants have found places in this country to which they seem well suited, the majority of them are lacking in some respects and offer very little advantage as competitors of the familiar plants already in cultivation. Most of the new forms,

FIG. 2.—The sunflower is now being used for ensilage. (After Linfield in Jour. Heredity.)

however, have certain features which make them appear promising. If their good qualities can be utilized by combining with them desired characters from the older domesticated forms, their full value may be realized. Introduction and improvement must go hand in hand. It is a waste of effort to produce something that already exists in some other part of the world. It is equally short-sighted to condemn a new plant or animal because it is not fully adapted to our particular conditions. If it has some

good qualities, these are materials out of which future additions of value may come.

Primitive man never took the trouble to cultivate a plant or tame an animal unless it already had usefulness as it grew in the wild. That apparently worthless plants and animals may have some valuable features has hardly yet been fully realized. The trifoliate orange is an unprom-

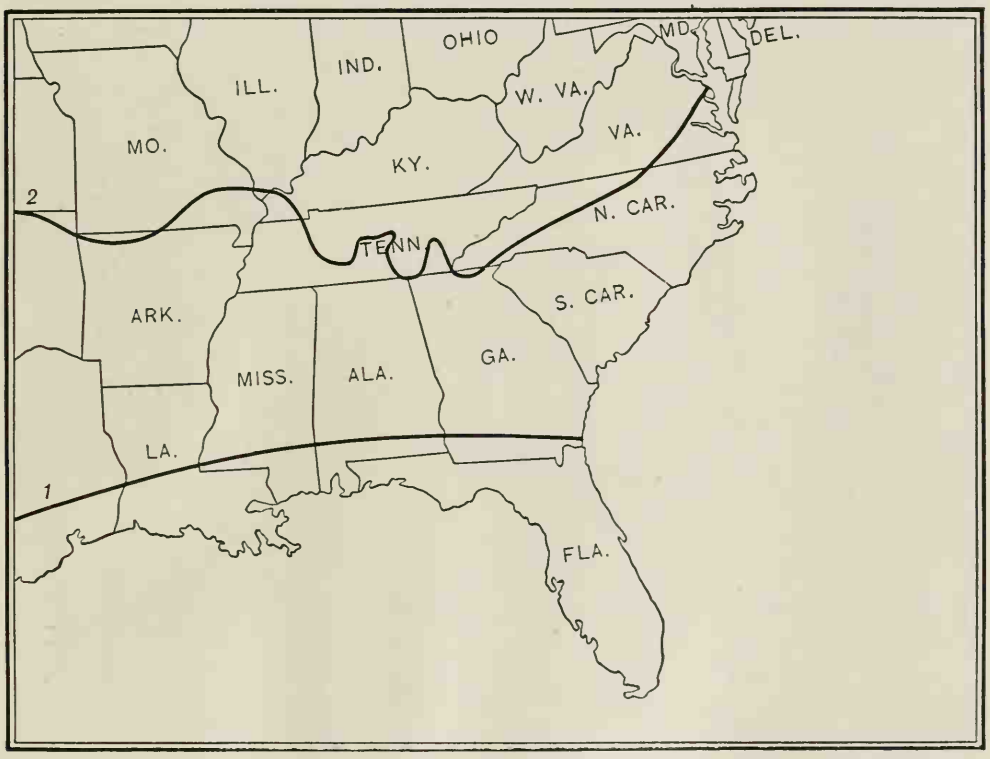


FIG. 3.—When first introduced, the culture of the velvet bean was limited to Florida and the land bordering the Gulf of Mexico. Earlier maturing varieties have extended its range of usefulness north from one to three million acres. (After Coe in Jour. Agron.)

ising near relative of the cultivated citrus fruits. It possesses the one good point of resistance to lower temperatures than these cultivated fruits can withstand. This character, combined as far as possible with the fruitfulness of the orange, has made possible the " citrange," a new fruit which extends the range of profitable citrus culture northward. When the velvet bean was first introduced, its usefulness was limited, on account of its long growing season, to

Florida and the land bordering on the Gulf of Mexico. After it had been grown for some time, a few early-maturing plants were found, and these were made the basis of several new varieties, which have extended the area of cultivation of this valuable plant several hundred miles northward.

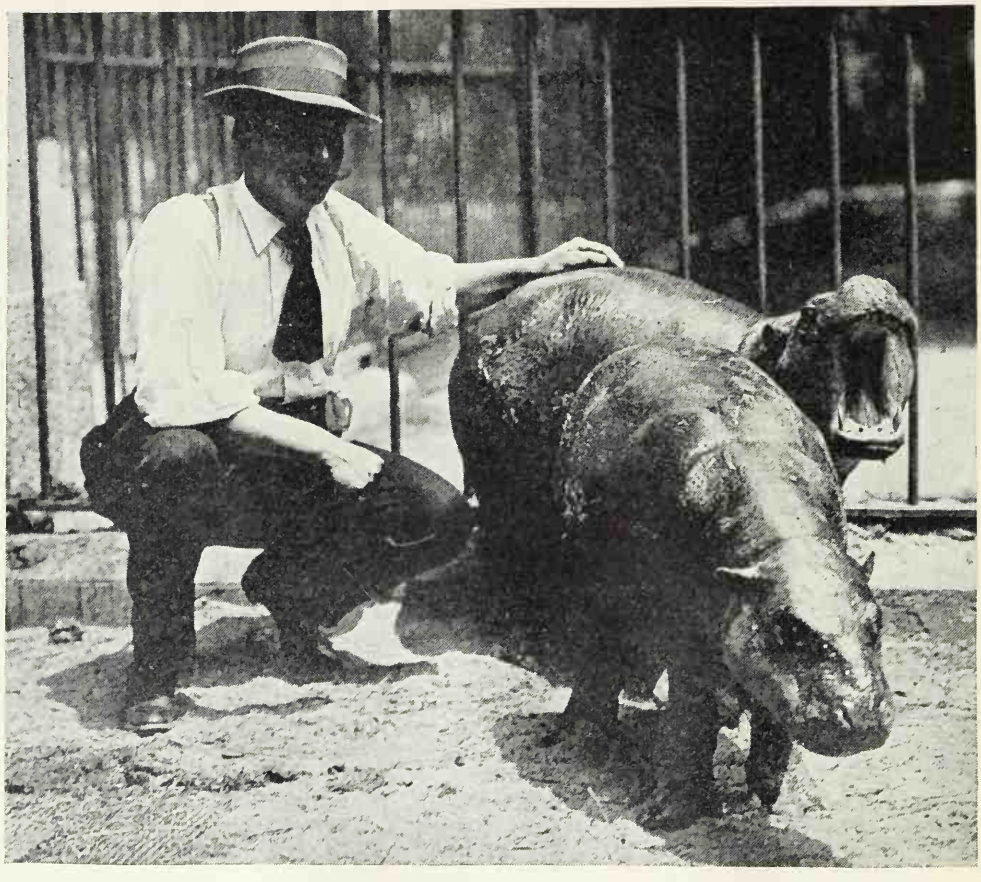


FIG. 4.—A small species of hippopotamus from Liberia, having possibilities as a meat producer in warm, swampy regions. (After Popenoe in Jour. Heredity, courtesy Zoological Society. Photograph by Elwin R. Sanborn.)

With the exception of the turkey in North America and the llama in South America, all our domestic animals have been introduced from the Old World. A noteworthy animal importation, which has attracted considerable interest in recent times, is the karakul, or fur-bearing sheep, from southwestern Asia. A small species of hippopotamus has been suggested as a possible source of meat in semi-

tropical localities. The zebu, or water-buffalo, from India, is being used in the South, on account of its immunity to disease. Another hardy immigrant from Tibet and Mongolia, the yak, can withstand cold and exposure, and is therefore promising for parts of Canada and Alaska. Both of these types, either by direct importation or after crossing with the common cow, may develop into valuable forms for certain localities. So far, the American bison has failed in competition with cattle; but a new animal, the cattalo, produced from the cross of bison and cow, has possibilities

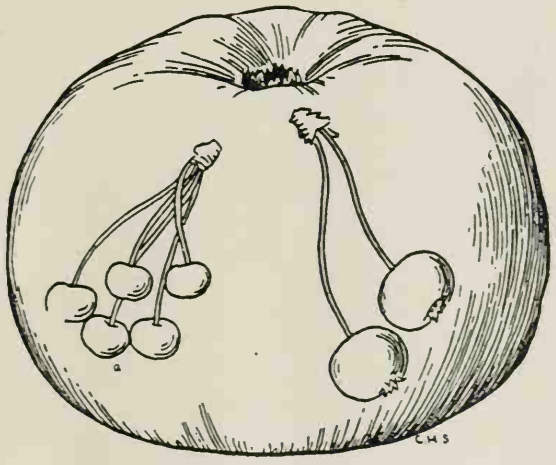


FIG. 5.—A commonly cultivated variety and two species of wild European and Asiatic apples. (After Freeman from Hodge in Kansas State Agric. College Farmer's Institute Bull., vol. 1, no. 2.)

for exposed ranges. The reindeer is another animal whose possibilities have not been fully developed.

As the existing varieties of cultivated plants and breeds of domestic animals are better in many cases, than those used in the past, further improvement may be expected. By permanently adding to the efficiency of the many plants which are useful as food, as fiber, or otherwise, and by increasing the capacity of animals to use food economically, the amount and value of the products obtained from the soil, both directly and indirectly, can be enhanced, and that with very little rise in the cost of production.

The beginnings of plant and animal improvement.—Migration, hybridization, selection—these have been the agencies by which present domesticated forms have been gradually adapted to the many diverse uses to which they are now put. The amelioration of wild species marked the beginning of civilization. The protection and cultivation of crops, for the purpose of insuring a more abundant harvest necessitated a community life in a more or less fixed abode. Probably the first plants taken from the wild

FIG. 6.—A European wild boar. (After Lush in Jour. Heredity.)

sprang up about the camps from seeds thrown out in the refuse. The advantage of having food grown close at hand must have appealed even to the most primitive man. When weeds grew up about these plants which were used for food, and threatened to choke them out, they were removed. The improvement of the resulting crop, due to this casual attention, was doubtless fully apparent in time, and led to the intentional planting of the seed; thus the domestication of plants began. Sooner or later it was realized that better plants grew from the seed of the best

individuals. In somewhat the same way, the improvement of domesticated animals started. Very early it dawned on man that it was sometimes easier to breed animals in captivity than to secure them in the hunt. The next stage was a realization that the most desirable animals tended to reproduce their kind.

In this way the great changes in animals and plants, which have taken place in the transition from the wild to the tame, were initiated. The alterations in many cases

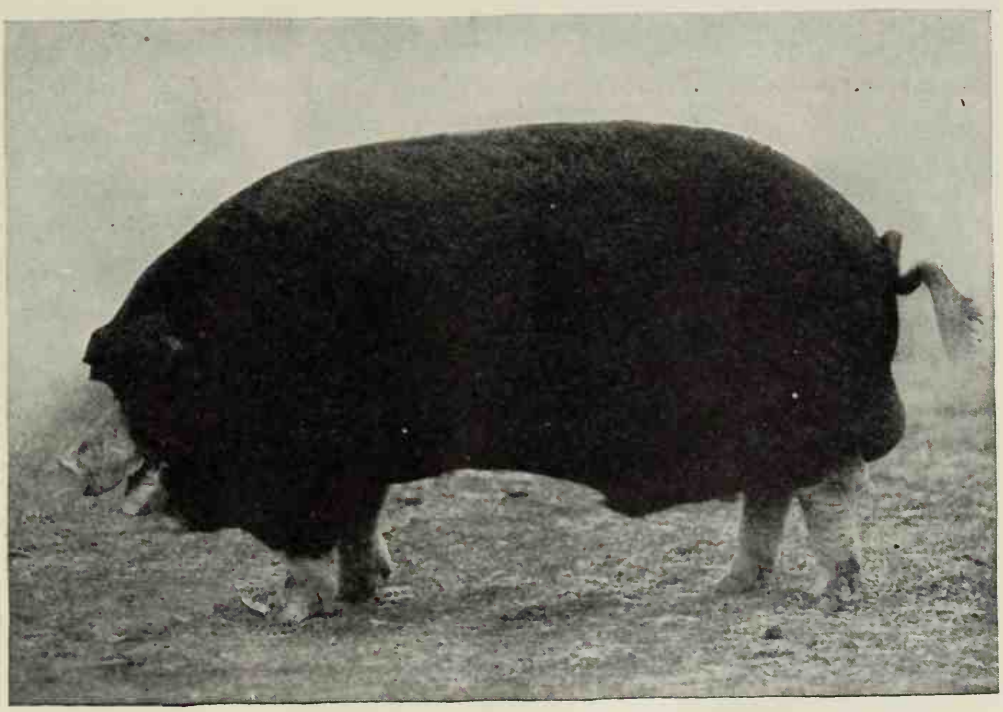


FIG. 7.—A representative Poland-China boar.

are vast. Compare the apple of to-day with the wild crab; the well-bred and well-fed pig with the wild boar of the forests. The length of time in which these differences have been brought about is not at all certain. In prehistoric times, many of the staple crops existed in much the same form as they do now. Grains of wheat have been found among the remains of ancient European and Asiatic civilizations. Recently a fossil ear of corn has been found in South America, differing in no essential from types grown

there to-day. This grain, therefore, has evidently been cultivated for a period that is measured by geological rather than historical time, as corn in its present form is not a plant which can maintain itself in the wild. The carvings of horses and cattle made by the early Egyptians and Assyrians show that their livestock had reached a plane of development comparable to our own.

A conservative view of future possibilities.—The great antiquity of the most important domesticated forms indi-

FIG. 8.—An early Egyptian carving, showing that the beef cattle of the Egyptians had many of the desirable qualities of the breeds of to-day. (After Burch in Jour. Heredity, courtesy of National Museum.)

cates that the creation of radically new types to compete with our staple crops and well-established breeds is not to be expected. If thousands of centuries have elapsed during the development of wheat, rice, and corn, which are the great contributions of Europe, Asia, and America, respectively, to the world's storehouses, what can we expect to do even in a lifetime? Let us not put too much faith in our superior knowledge, nor hope to accomplish in a few years what primitive man, at all times confronted by pos-

sible famine, has taken uncounted epochs to do. The fear of starvation develops very keenly the search for edible food plants and new variations, whereby their production can be increased. At the most, we may hope to improve somewhat the forms already domesticated and to bring in others from the wild for certain special purposes.

The greatest encouragement for plant betterment comes

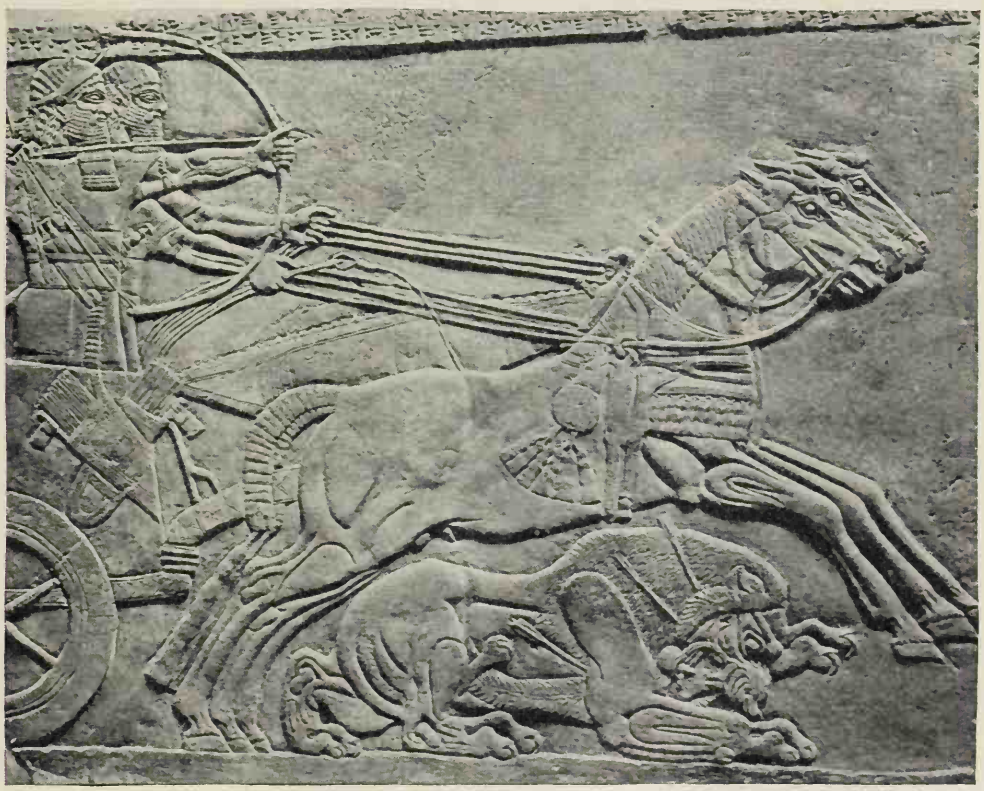


FIG. 9.—Assyrian horses, six centuries before the Christian Era, had reached a high plane of development. (After Burch in Jour. Heredity, courtesy of National Museum.)

from what has already been done with aimals. Animal breeding has been brought to a higher plane of development than plant breeding, and there are several good reasons for this. From the first, sex in animals has been obvious. The essential similarity of sex in plants to that in animals was not clearly seen until the close of the seventeenth century. Of more importance is the greater value of the individual animal as compared with that of the individual

plant. In the former, the good and bad points are more apparent and selection has always been more rigid. The great improvement in animals which took place during the establishment of many of the existing breeds of livestock, in the seventeenth and eighteenth centuries in England and the Continent, came about largely through the realization of the importance of the pedigree. The criterion of selection was shifted from individual appearance to past performance. So extensive and carefully kept are the pedigrees of pure-bred livestock that the ancestry of many herd leaders can be traced two hundred years back.

Plant breeding has never been raised to this plane of efficiency except with a few plants. Pedigree records of naturally cross-fertilized plants for more than a few generations are almost unheard of. Corn, the most valuable plant in the Americas, is still largely selected on the basis of the individual appearance of the seed ear. With this plant, very little serious attention is given to performance and practically none at all to the qualities of the pollen parent. In comparison with animal breeding, some of the practices in plant improvement are two hundred years behind the times. For the most part, our vegetatively propagated fruits and flowers are Nature's children taken from the highways and byways because they are the best so far available.

Early history of the art of breeding.—The beginning of interest in the purposeful creation of new forms of plants and animals is obscure. The early cultivators of the date palm were probably the first to practice artificial pollination, and indirectly this helped them in originating new varieties. The records show that the Chinese, in very early times, gave careful attention to the discovery and propagation of better kinds of rice. The first systematic endeavor to create new varieties of plants on a large scale grew out of the intense interest aroused in bulb culture in Holland during the seventeenth century. Hyacinths and tulips had recently been introduced into that country, where conditions

were well suited to their growth, and they soon became a fad. The enormous prices paid for new sorts is a matter of historical interest. It led to the production of an amazing array of varieties, running into the thousands in a short period of time. This was made possible by the large number of plants grown, by the conspicuous flowers, which made it easy to recognize new variations, and by vegetative propagation, which enabled new forms to be kept pure. The artificial distribution of pollen and the growing of the plants from seed were necessary for the great diversity in size, shape, and color that was so quickly obtained. From this time, interest in the production of new forms in all manner of plants grew rapidly. In the eighteenth century, several men stand out as originators of new varieties of value; but the world owes its greatest debt to the many seedsmen, nurserymen, and plant propagators in general, for the abundant variety of economic plants everywhere available. It is due to their enterprise, rendered very keen through ordinary business competition, more than to anything else, that new varieties have been discovered, multiplied, and offered to the whole world to try and to use as far as they have been found to have merit.

Although the Arabs, in early times, gave unusual attention to the breeding of their horses, systematic selection involving a continuous record of ancestry was not practiced until the present familiar breeds of cattle and horses began to take form in western Europe, about two hundred years ago. Most of the improvements in animals have come from the efforts of individual farmers, some of whom have profited well from their skill and patience while others have not. All, however, have worked with the pleasure that comes from originating new and more useful forms of life.

The science of genetics.—Most of the great improvements in animals and plants were made before there was any definite knowledge of the process of inheritance. The middle of the past century saw the real beginning in the scientific study of **heredity.**

Heredity is generally understood as the tendency of offspring to be like their parents. The study of heredity is a part of the broader field of biology known as **genetics.** The word genetics was first used by Bateson and is derived from the Greek γεν, meaning "become." Genetics deals with the physiology of heredity and variation; in other words, it deals with the origin of individuals and varieties, as contrasted with the related study, evolution, which is concerned with the origin of species and races. Evolution has to do with changes which occur during long periods of time, geological epochs. Genetics deals with the changes which take place from generation to generation and the means by which features and traits are reproduced in different individuals. As defined by Babcock and Clausen, "Genetics is the science which seeks to account for the resemblances and differences which are exhibited among organisms related by descent." How do individuals from the same parents, starting from small particles of living matter which visibly are alike, reach their adult form resembling each other in many ways but differing in others? The answer to this question is sought in various lines of investigation. These are the methods of observation, of experimental breeding, of cytology, and of experimental morphology.

The method of observation.—Much can be learned by studying aimals and plants as they live under natural conditions. Those which are slow in maturing can not be used satisfactorily under controlled conditions on account of the length of time needed. It is often impossible to have large enough numbers under experimental control, and this necessitates the basing of conclusions upon individuals naturally reproduced. The extensive observation of similar species in different parts of the world was the principal evidence that Darwin (1809–82) used in formulating the doctrine of evolution by natural selection. The discovery of marked differences in plants growing in the wild, supplemented by controlled experimentation, led De Vries to

formulate the mutation theory. Observations, to have value, must usually be based on large numbers, mathematically treated in such a way as to remove doubt as to the accuracy of the conclusions drawn from them. Statistical methods applied to biological problems have developed into the special field of biometry. This line of investigation was started by Quetelet (1796–1874) and later continued by Galton (1822–1911), who, after measuring the characters of a large number of individuals in successive generations, formulated the laws of ancestral inheritance and filial regression. According to the former, each parent on the average contributes one-fourth, each grandparent one-sixteenth, and so on, to the total inheritance of the individual. According to the law of regression, the offspring tend to return to the average of the race to which they belong, and, considering all the individuals together, they deviate from the mean only two-thirds as much as their parents differ from it. These laws are descriptive of the group as a whole and can not apply to particular individuals. This disadvantage of the observational method renders it more suitable for dealing with groups than with individuals. Moreover, observations unsupported by experimental verification have in the past led to erroneous opinions. Thus, the evidence seemed very clear to earlier biologists that the variations arising from differences in the environment were inherited. When the matter was put to experimental proof, adequate support for this opinion was not obtained, with the indication that these variations can be better accounted for in other ways.

The method of experimental breeding.—Probably more information has been obtained by the breeding of animals and plants under control, whereby the characters of all individuals in successive generations can be known and compared, than by any other method. Practically nothing was known about the process of heredity until Mendel (1822–1884) applied this method to the garden pea; and his success was due largely to the fact that he followed single differences in plant structure from generation to

generation in individuals that were self-fertilized and cross-fertilized. This controlled breeding is generally spoken of as the pedigree culture method and has been widely used with a great variety both of animals and of plants. Its special advantages lie in the fact that differences due to inequalities in the environment can be overcome to a certain extent, and that the results obtained can be verified. Its principal limitation is the small numbers which are usually available. The results must be treated statistically, as in the method of observation, with due regard to errors which arise from chance deviations.

The method of cytology.—With the development of the microscope, attention has been paid to the internal structure of living matter in the endeavor to locate the material substances which are transmitted and distributed from one individual to another in reproduction, and which make up their inheritance. Cytology, the study of cells, is a special method of observation. Owing to the exceedingly small size of the units of plant and animal structure, and the fact that very little can be seen until the tissues are properly prepared by killing, fixing, and staining, the same individuals can seldom be both examined for internal structure and used for breeding purposes. But, by comparing the observations made by means of the microscope with the known breeding behavior of similar individuals, the greatest advances have been made, and these advances have culminated in an understanding of the mechanism of heredity.

The method of experimental morphology.—Although the main features of the process by which traits are passed on by inheritance from individual to individual are known, very little is understood as to the means by which the potentialities in the egg find expression in the adult. This is the field of developmental mechanics which includes such studies as embryology and ontogeny. Since the whole organism can often be regenerated from a smaller part in many forms of life, as when we take a cutting from a rose bush or break an earthworm in two, it is obvious that the

potentialities of the entire individual are retained in all, or nearly all, of the many different parts of such organisms. Although not all plants and none of the higher animals have the power of reduplicating the whole organism from a smaller part in the adult form, there is a stage in development in all forms of life up to which complete regeneration is possible. Experimental morphology seeks to discover how the determiners of heredity, which are passed from part to part as well as from individual to individual, are able to control the development of different organs in their proper places.

This line of investigation is closely dependent upon the physics and chemistry of organic substances, and the complexity of these substances has, up to the present, made progress very slow. But it is probably only by a clearer understanding of the composition of living tissues, and particularly those that are involved in hereditary transmission, that it will be possible to account for the primary occurrence of heritable variations and perhaps control their frequency and nature.

Each of these main lines of investigation has its advantages and limitations, and all are subject to error. As a result of the application of knowledge gained from all sources, the mechanism by which the hereditary determiners are transmitted from generation to generation and recombined is now understood in its most important features. Many perplexing problems still remain to be solved. There is, for instance, no clearly established way by which permanent variations in any direction can be originated or even predicted. New methods of attack will undoubtedly be developed in the future.

Prerequisites for the study of genetics.—A satisfactory understanding of genetics requires a general knowledge of life processes as given in introductory courses in botany and zoology. Agricultural genetics is largely confined to the higher organisms, and particular attention should be given to anatomy and classification, and to the physiology of

growth and reproduction in such organisms. However, these can only be thoroughly understood by a general acquaintance with all forms of life. The control of diseases and pests by the production of resistant varieties is helped by a knowledge of the parasites which are distributed throughout the plant and animal kingdoms, as well as of their hosts. While a considerable working knowledge of genetics can be had with the use of only the simple forms of mathematics, the student who expects to go very far in this subject will find the various forms of refined statistical methods and a knowledge of the mathematical principles upon which they are based of distinct advantage in properly interpreting the facts of heredity and variation.

The application of genetics.—Heredity is a property of all forms of life, and all the biological sciences have been greatly clarified by the recently acquired knowledge of genetics. The study of evolution has the same problem as that of genetics, namely, the mode of origin of hereditary differences. Sociology, history, anthropology will be better understood when considered with the facts of racial heredity and variation. The science of genetics has its most direct application in eugenics and in plant and animal breeding. Eugenics, as defined by Galton, "is the study of agencies under social control that may improve or impair the racial qualities of future generations, either physically or mentally." Since the operation of the laws of heredity and variation are the same for man as for the higher animals, eugenics is a special field of applied genetics. It is to agricultural problems that genetics has its most immediate application. Breeding is defined as the art of improving economic forms of life by hybridization and selection. Every advance secured by these means in the inherent productive capacity of plants and animals is a permanent gain to the world, making necessary supplies more abundant and more easily obtained.

It is no wonder then that this new science of genetics, with its promise of human betterment, is being followed

with an enthusiasm almost without parallel. Already plant and animal breeding is being put on a more efficient basis. Notable improvements in such valuable plants as wheat and cotton have recently been made by the application of proved principles. Methods are available by which much of the uncertainty attending present practices in animal breeding can be removed. The creation of new and better kinds of domesticated animals and plants has had a great appeal to the imagination and has in some cases raised hopes which are impossible of fulfilment. Not the least contribution of genetics has been a clearer realization that there are many things, often proposed, which probably can not be done. Not only is a thorough knowledge of the principles of genetics necessary to advance real achievement, but a proper understanding of the limitations of plant and animal improvement is equally useful in minimizing wasted effort. It is in the hope of contributing to the realization of such limitations and the accomplishment of actual possibilities that the principles and methods set forth in the following pages are offered.

CHAPTER II

THE RELATION OF ANIMALS AND PLANTS TO THEIR SURROUNDINGS

EVERY individual is the resultant of the action of three forces: inheritance, environment, and training. Inheritance is what the organism receives at birth; it can not ordinarily be changed thereafter. Environment includes all the influences which have their origin outside of the body, whether favorable or injurious. Of these, food, temperature, light, and parasitism are the most obvious. Training is what the organism does for itself by using its inheritance and environment. Thus the speed of horses is developed by running. Skill of any kind comes largely from practice.

Only potentialities transmitted.—Certain peculiarities are said to be inherited. But the distinguishing features of a plant or animal are never transmitted bodily. There are no feathers in the egg of a bird before incubation. The seeds of many different species of plants are much alike in shape, size, and appearance, but have a totally different inheritance which governs their growth. *What is handed on from one generation to the next is the power to develop certain characters in a suitable environment and by proper training.* If either environment or training is modified the result will be different. Therefore, the expression of heredity differs according to the conditions in which the individual grows. It is like an exposure on a photographic film. The picture is there. No developer can change its inherent character, but proper development may make of it a beautiful picture while careless handling or the use of wrong solutions may mar or ruin it. But the best developers and the greatest skill can not make a good picture out of a poor exposure.

The relative importance of inheritance, environment, and training.—Inheritance is fixed. Environment and training are always working throughout the life of the individual to make it what it is, although the effects are more pronounced during the early formative period of growth. The relative importance of the three influences—inheritance, environment, and training—are often and vainly dis-

FIG. 10.—Effect of spacing upon the growth of corn. At the left, corn plants properly spaced in hills. At the right, plants from the same kind of seed, badly crowded. (After Blakeslee in Jour. Heredity.)

cussed. Such discussion is somewhat like argument as to the most important leg of a three-legged stool. For man, all are essential and none can be neglected without having a marked effect. As training has no significance for plants and little for most domestic animals, all external influences for them, including training, may be here understood in the term environment.

In the past, more attention has been paid to external influences because their modifying effects for better or worse

are easily and quickly seen. The ways in which the internal forces of heredity operate to limit the capacity to grow and to produce are complex and are not easily understood. Nevertheless, given the same environment, the ability of different individuals to utilize this environment is absolutely dependent upon their hereditary constitution. Increased production by improvement in the cultural factors is usually expensive and the outlay must be continued each year. Good heredity, in most cases, aside from the initial cost, works continually without further expense. Effort is now being more and more directed to utilize heredity to the fullest extent; but good heredity, without the opportunity to express itself, is of no value.

Effect of the environment upon plants and animals.— An examination of the effects of the environment on plants shows that certain kinds of characters are more directly influenced than others. It is easier to change the size of plants than the habit of growth. One may increase or decrease the number of flowers according to the type of soil in which the plant is grown or the way in which it is pruned, but it is rarely possible to change the color or form of the flowers by such treatment. In general, those characters susceptible of modification by external influence are quantitative in nature. One plant may flower early, the other late. But the main details of the plant are seldom changed beyond recognition by differences in culture.

Plants which are crowded or are raised on poor soil are small and spindling and may not flower or set seed. The same seed, sown on good soil and properly spaced, gives a far different result, as shown in Fig. 10. A tobacco plant may be grown in a small pot in the greenhouse, where it will flower and produce a few seed pods when only a foot or so in height. Seed from this plant, grown in the open, will give normal plants that may grow 8 to 10 feet tall and produce hundreds of seed pods.

Bonnier, a French botanist, divided a single plant of the common dandelion into two parts. One of these halves was

planted and grown for some time at a high altitude in the mountains. The other was grown in fertile soil in the

FIG. 11.—Two halves from the same dandelion plant, one grown at a high altitude in the mountains, the other in fertile soil in the valley. (After Bonnier.)

valley. The two plants soon became markedly different, as shown in Fig. 11. The mountain plant was about one-

tenth the size of the other and differed in practically every part.

Animals are equally sensitive to their surroundings, but the changes which can be induced usually affect only size and rate of maturity. The coat pattern or color is seldom or never modified. The Herefords can be distinguished from the Galloways, no matter how poorly or how well

FIG. 12.—Differences in size, due to feeding. These two animals were calved on the same day and possessed essentially the same capacity to grow. The larger individual was fed generously and weighed 1610 pounds at two years of age. The smaller was given a very limited ration and after two years weighed 361 pounds. (After Mumford in Breeder's Gazette)

they are cared for. The quick actions, light weight, and non-setting characteristics of the Mediterranean breeds of poultry are racial traits and can be very little influenced by external conditions.

Distinguishing between hereditary and environmental variations.—The best proof of purely external modifications is found in plants propagated vegetatively from the same source or even in differences in parts on the same plant.

Potato plants in the same field differ greatly in productiveness. The foliage which first appears on some plants differs in a remarkable manner from leaves produced later. The mulberry, on young, vigorous, growing shoots, puts out leaves which are not cut at the margins. Later leaves are deeply cut and divided. The growing conditions at the time the leaf buds are formed control this.

Since it is quite obvious that variations do occur on plants grown in different surroundings, and even on different parts of the same plant, it is important to know which of these variations are due to heredity and which to external effects, and in the latter case how permanent these changes are. The plant and animal breeder also wants to know whether or not there is a cumulative effect of external conditions. Can an individual grown continuously under good surroundings be expected to give better progeny than one raised under poor conditions? This is an important question and one that can not be lightly answered.

Effect of external conditions upon the following generations.—There is a very general opinion that external conditions can modify plants and animals in such a way that their progeny is affected. For a long time it has been the practice to dehorn cattle and to cut off the tails and ears of pet animals. There are breeds of hornless cattle and tailless cats which are hereditarily without the undesired organs. Study of the evidence gives no indication that the hornlessness or taillessness arose as a result of such mutilations. If the hereditary loss of these organs were due to the continued removal of the objectionable parts it would be reasonable to suppose that their disappearance occurred gradually. Such is not the case, however, as hornless cattle, at least, are known to have originated from fully horned stock.

Weismann performed an experiment along this line by cutting off the tails of mice for nineteen generations in succession. At the end of the experiment there was no indication hatever that the tails of these mice were becoming

any less well developed, and no tailless mice were produced. Circumcision has been practiced by certain sects for thousands of years with no apparent inherited effect. Mutilations resulting from accidents are common to men and women; fortunately, their children are not thereby deprived of useful organs, otherwise the earth would be populated by races of cripples.

It may be argued that the mutilation practices or experiments have not been carried on long enough to produce any appreciable effect. It is thought that plants or animals exposed for very long periods of time may show some effect of the environment. For example, the characteristic habit of growth of a conifer in cold climates is a straight central trunk with sloping branches. The resulting form is an undoubted advantage, as it allows accumulations of snow to slide off harmlessly without breaking the branches. The question may be asked, "How did the trees come to have this habit of growth, since conifers do not have it everywhere?" Did the constant weight of the snow, pressing on the branches and inclining them downward, finally impress this feature on the trees so deeply that it came to be inherited? It is not necessary to assume this. It is as reasonable to suppose that trees differed in the position of their branches because of other than external influences, just as they differ in every other respect. In the snow countries, those trees with drooping branches suffered less from breakage and were thereby better able to produce seed and propagate their kind.

We can leave it to the evolutionists to decide which is the correct interpretation. They may differ in their opinions as to how these results were brought about, but they are all agreed that organisms often do remain the same, without showing any visible permanent effect of their surroundings, for very long periods of time. Certain fossil insects, well preserved in amber from geological periods whose ages are reckoned by millions of years, differ in no perceptible way from individuals of the same species alive

to-day. If some organisms retain their characteristics through geological epochs, it is wholly improbable that domesticated animals and plants, subjected to the ordinary differences of their surroundings during a relatively few generations, can be appreciably altered in their hereditary constitution. Heritable variations, apart from the great changes made possible by hybridization, do occur from time to time, due to other causes unknown. There is also some experimental evidence, to be discussed later, to show that permanent changes can be brought about by special agencies. But, for all practical considerations, it can be stated positively that the usual differences which are acquired during the life of the individual are not passed on. This means that the offspring start from the same place from which their parents started, neither helped by the influences which favored them during their lifetime nor hindered by their obstacles.

Independent experiments by Bagg, by MacDowell, and by Vicari show that successive generations of rats and mice, trained to go through a maze to get their food, do not learn any more quickly than other animals whose ancestors have never been trained. These results flatly contradict reports, widely heralded in the popular press, that the offspring of trained animals learn how to do certain things more quickly than the offspring of other individuals which have had no training. An opportunity for error in such experiments lies in the selection for breeding of the individuals which respond most readily to the training. These are the inherently more intelligent animals, whose offspring, owing to their better inheritance, would be expected to respond more rapidly than the offspring of unselected stock.

Insulation of the reproductive tissues.—Although each individual is destined to die when its life cycle is completed, a part of that individual may live on in the next generation, and from that to the next and so on indefinitely. Whatever the substance is, that is transmitted from one generation to the next in the fertilized egg or other parts used for

reproduction, that substance carries the inherited potentialities. This reproductive material has the power of self-perpetuation and in each generation builds for itself a new body to nourish and protect itself from the adverse influences of its surroundings. Weismann was the first to emphasize the fact that this continuing life stream, or **germplasm,** as he called it, was effectively insulated from the outside world, and that the changes made in the body, or **somatoplasm,** can not be transferred to this germplasm and the embryo organisms formed from it.

In the more familiar animals, only the reproductive glands, the **gonads,** furnish the material from which the embryos are formed. In some animals, the tissue which forms the gonads is differentiated at a very early stage in the developing embryo. Here a direct continuity from egg to egg can be seen. The embryo develops directly from the germinal tissue and not from the body tissues. The function of the latter is merely nutritive and protective. In this way Weismann argued that there was no way in which acquired characters could obtain a representation in the material which reproduces the next generation, and that therefore such characters could not be inherited any more than the water that has passed over the dam could affect a stream that had been diverted from above the dam.

On the other hand, many of the lower animals may be cut into small pieces, any one of which, under suitable conditions, may regenerate the whole animal with all its parts. Some plants can be propagated by parts of leaves, stems, or roots. Therefore, it is obvious that no clear distinction can be made between body tissues and reproductive tissues. The evidence indicates that every part of the body carries all of the inherited substances and is potentially able to reproduce the entire organism. The reason that many parts can not do this is that they have become too specialized for other purposes.

The essential feature of Weismann's germplasm theory is that the ordinary influences exerted by the environment—

influences which profoundly change the external features of the individual, without destroying its ability to reproduce —leave no more impress upon the transmission of the inheritance from one generation to the next than the surface waves leave upon the ocean's depths.[1]

Modifications which are carried over from one generation to the next.—While the reproductive tissues are well protected from external influences, certain modifications from the outside are handed on temporarily from one genration to another. It is known, in the case of animals, that certain infectious diseases, if present in the mother, can reinfect the offspring before birth and so be passed on from generation to generation. There is no evidence that the inheritance has been changed, but the effect is the same. Similarly in plants, it has been proved that peach trees affected by the disease known as " yellows " will transmit this disease in the buds used for propagation. An infected bud inserted in a healthy tree will produce the disease in all parts of the tree, and the tree in turn will transmit it if such trees are used for budding material.

Immunity to disease and the effects of certain poisons are temporarily handed on. In somewhat the same way, markedly unfavorable effects of external conditions may be passed on, to a limited extent, from one generation to another. As an illustration of this, two lots of seed from one ear of corn were planted at different times. One was sown early. It grew normally and ripened its seed in good condition. The other lot was planted very late. The plants were smaller, flowered in the cool weather of the fall,

[1] Because the reproductive cells in most animals are localized in special tissues, zoologists as a rule readily accept the essential principle of the germplasm theory. But since plants are readily reproduced from nearly every part, botanists are less disposed to accept this theory. When one kind of plant is grafted upon another, neither form exerts any influence upon the reproduction of the other; and in the special cases known as chimeras, tissues of different plants come to grow together and persist indefinitely in vegetative propagation without altering each other. These phenomena show clearly that the germplasm is as impervious to change from external influences in plants as in animals.

and were barely able to ripen seeds, which were small, shrunken, and dull-colored. When both lots of seed—the one properly developed, the other very poorly matured—were planted side by side at the same time, there was a marked difference from the start. The well-formed seeds germinated promptly; the seedlings were large and grew normally. The poor seeds produced small, weak seedlings, which were slow in appearing and were kept alive with difficulty. The plants thus handicapped at the start were never able to make up the difference during the season, and the seeds produced in the fall were again smaller and less well developed than those from the good seed. The differences were not so great as the year before, but were great enough to handicap somewhat the plants the next year. After the second year, in which the two lots were grown under equally favorable conditions, all differences were lost. There is, therefore, in this case, no permanent effect; but the temporary influence carried over from one year to another is very important to the man who is endeavoring to grow the best crops.

Several years ago, the New York Experiment Station tested the result obtained by growing tomato seed of green and ripe fruits borne on the same plant. When the differences in the maturity of the fruits selected for seed were marked, the progeny was found to be noticeably affected. The plants from the immature seed were smaller and yielded less fruit than the plants from normal seed. The immature seed also produced fruit which ripened earlier, probably due to the lessened vegetative vigor and reduced foliage of the plants. Here also, the unfavorable effect of immaturity was carried over from one generation to another, but no one should expect to produce an early variety of tomatoes by such procedure.

T. H. White at the Maryland Station investigated the influence of large amounts of fertilizer upon the progeny of the Red Cherry tomato. It was found that a larger growth of foliage and fruit, produced in the parents by the

extra fertilization during six years, was apparently transmitted to the progeny for at least three generations after the treatment was discontinued. This is another illustration of the carrying-over from one generation to another of changes produced by different culture. There is certainly no proof that the hereditary construction was permanently altered. Logically, it is difficult to see how lasting alterations could be occasioned by a few years' difference in treatment. If subjection to extraordinary fertilization during two or three years can change the tomato, what becomes of the influence of the previous hundreds of years of ordinary culture? If plants are susceptible to germinal modification by their external surroundings it would be expected that the long periods of time in which the plant grew normally would have more effect than a few years of unusual treatment. At the most, a few years' difference in the surroundings could modify the hereditary composition of the progeny very slightly, and this small change in most cases could not be distinguished from the carrying-over effect previously illustrated. Practically, it is not necessary to distinguish between the two. But it is decidedly worth while to know that plants or animals can not be permanently impaired by being subjected temporarily to unfavorable conditions. Neither can their heredity be constitutionally improved by growing them in an especially favorable environment.

The two functions of the seed.—It is therefore necessary to distinguish very carefully between the two functions of the seed or other parts of a plant used for propagation. One of these is to store up an adequate supply of food, to enable the young plant to have a proper start in life. The other is to transmit the individual qualities inherent in the plants which comprise its ancestry. Failure to distinguish clearly between these two functions has led to much confusion.

Importance of a favorable environment.—Variations in the size of the seed alone, with some plants, have con-

siderable effect upon the result. Cummings, at the Vermont Station, has demonstrated with various vegetable crops that the size of seed is a matter well worth taking into consideration. Size alone is not a sure criterion of the amount of energy carried in a seed; but, by separating the large and small seed of several different varieties of the common quick-growing vegetables and planting these under like conditions, it has been found that the crops grown from these two kinds of seed differ greatly in some cases. Especially is this true of the radish, as shown in Table I,

TABLE I

THE INFLUENCE OF THE SIZE OF SEED IN THE RADISH UPON THE CROP HARVESTED

Data from Cummings, in Vermont A. E. S. Bull. 177

Variety	Size of Seed	Number of Plants	Total Weight of Roots in Grams	Average Weight of Roots in Grams
French breakfast...	Large	78	890	11.4
French breakfast...	Small	55	425	7.7
Scarlet globe.....	Large	53	765	14.4
Scarlet globe.....	Small	56	573	10.2

which is one of the quickest-growing vegetables. As the time between the planting and the harvesting is very short, it is to be expected that the nourishment placed in the seed will be a decidedly important factor in the ensuing crop. With other plants, which are longer in maturing, differences in the seed tend to be obliterated before harvest. Frequently, however, slight differences at the critical stages of a plant's existence may make noticeable differences throughout the whole period of development, and this effect may extend to later generations. Animals are particularly responsive to favorable conditions for growth. Feed and care can make profound changes, particularly during their early life. Because embryonic mammals are nourished for

so long a period before birth, the physical condition of the mother is of great importance. The herdsman gives his breeding stock the best feed and care. Many poultrymen take the largest eggs for hatching. This is not done to improve their heredity, but in the hope of giving the young the best possible start in life.

Nothing, therefore, should stand in the way of securing the best developed seeds possible. With plants propagated vegetatively, it is equally important to obtain well-developed, healthy material from which to select buds or grafts. This is merely a common-sense, sanitary precaution. But

FIG. 13.—Squash seedlings from large (left), small, and medium (right) seeds. (After Cummings in Vermont A. E. S. Bull. 177.)

in using such well-developed seeds and healthy grafting stock, one should not be deluded into thinking he is thereby permanently improving the variety. If necessary, plants which have been temporarily subjected to unfavorable surroundings can usually, by proper treatment, if no infectious disease is present, be reinvigorated with no lasting injury whatever to their inherent hereditary qualities. The same statements apply to animals.

In selecting individuals to be the basis of a permanent improvement, it is necessary to distinguish between variations which arise in the inheritance and those which are environmental or external in origin. This is the task of

the breeder, and very often it is a difficult one. Good growing conditions are sometimes a hindrance in that they tend to obscure the heritable differences sought for. The place to look for cold-resisting plants is in fields which have been severely damaged by cold. To find disease-resistant types it is necessary to have the plants infected with the disease-producing organisms. In the same way, to obtain plants which are inherently better able to grow and to yield, it is essential to seek for them in places where they have not been specially favored by their surroundings. The obvious effects produced by good heredity and those produced by good environment are often alike. It is impossible to be sure which is the cause of the good appearance of individuals until their progenies have been grown and compared with other progenies.

The progeny performance test.—The selection of the parents according to the performance of their progeny is the basis of all intelligent improvement. Generally the behavior must be tested for more than one year. This involves a registry of parentage and a record of performance through several generations, obtained in such a way that the ever-present variations in the plant's or animal's surroundings do not obscure the hereditary differences. Large enough numbers must be grown to make the averages based upon them significant. With plants, differences in soil have to be overcome by having replicated plots in different parts of the field. Unequal competition between adjoining plots can be avoided by planting guard rows. Animals should be carefully graded as to size and otherwise handled in such a way as to permit equal opportunity to grow. Only by having the environmental influences the same for all can the inherited capacities be judged.

The breeder's problem.—It is now clear that the problem that confronts the breeder is to find out the hereditary constitution of the individuals with which he is working. In the past, the external features only have been compared. This has often led to much confusion, because the visible

features are not a reliable guide to the internal constitution. For example, a black cow mated with a black bull may produce a red calf. Two white-flowering varieties of phlox are known to give colored flowers when crossed. Therefore, the statement that by heredity " like produces like " is not always true when applied to visible features.

CHAPTER III

HOW LIVING ORGANISMS REPRODUCE THEMSELVES

THE flowers of the individual date palm, as well as those of the mulberry, poplar, hop vine, asparagus, hemp, and spinach, produce either pollen or seed, but the two are not ordinarily borne together on the same plant. Seeds are produced only when pollen is brought to the seed-bearing flowers. From the fertilized seeds, pollen-bearing and seed-bearing individuals are produced in about equal numbers.

One staminate date palm produces enough pollen for about twenty pistillate trees, if this pollen is distributed by hand, which is easily done as pollen is produced in abundance and the fruit is borne in large clusters. It was soon discovered that it was a waste of land to grow as many unfruitful trees as came naturally from the seed. Artificial pollination of this royal fruit tree from a small number of pollen bearers has been the custom since very early times, as is evidenced in prehistoric Egyptian drawings picturing the date palm and the process of pollination. Although it is apparent that the ancients had some conception of the similarity of this phenomenon in plants with sex in animals, nothing was done in the way of a wider application of this idea until the time of Cammerer (Camerarius). In 1694, this sagacious investigator proved that pollen is necessary for seed production and showed that the phenomenon of sex is essentially the same in plants as in animals. Since that time, investigation of the methods of reproduction of all forms of life has been actively pursued.

Methods of propagation.—Sexual reproduction was not the primitive means of propagation. Many simple organisms multiply by division in which there is no union of two

individuals. Going a little higher in the scale, it is found that some forms reproduce by means of *spores* which are

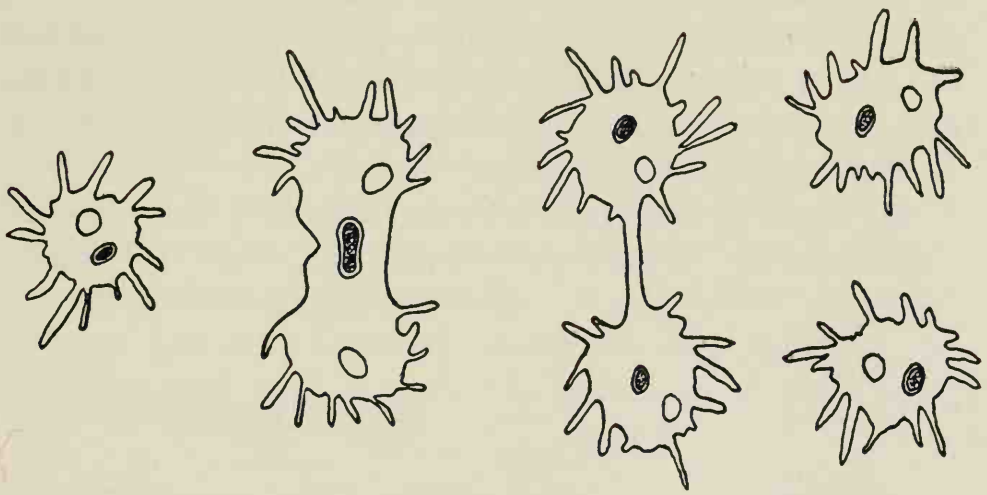


FIG. 14.—Reproduction by simple division in the amoeba.

specialized structures set apart for disseminating the organism, but here also there is no fusion of two of these

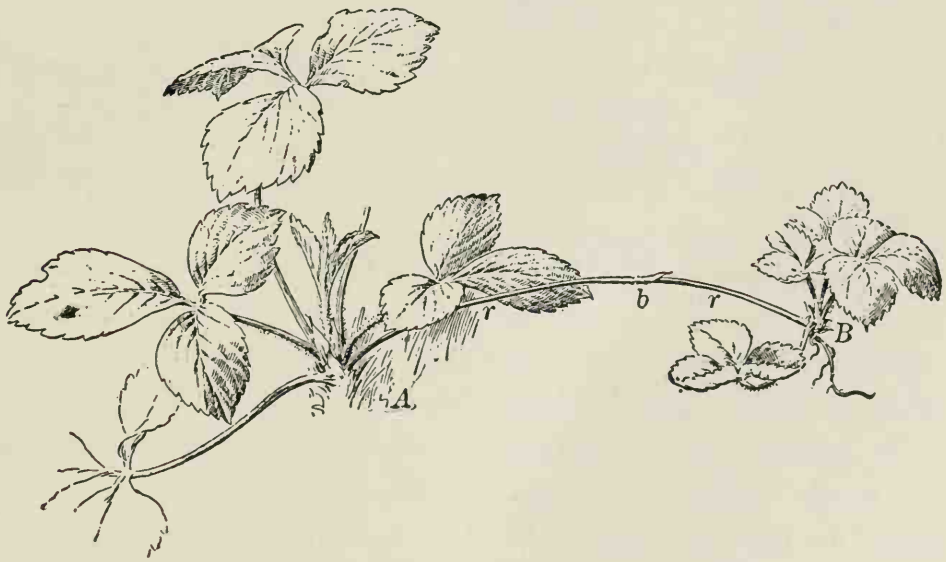


FIG. 15.—Vegetative reproduction by means of runners in the strawberry. (After Bergen and Caldwell in "Practical Botany," courtesy, Ginn & Co.)

spores as in true sexual reproduction. Nor has asexual reproduction been entirely superseded even in the higher

plants; many species, in which the sexual union of two individuals is the rule, still multiply themselves vegetatively by division of parts like bulbs and tubers. Various plants send out underground stems, as quack grass (*Agropyron repens*), or runners, like the strawberry. Others root at the tips of branches and spread themselves rapidly in that way, as, for example, the brambles.

While all of these plants retain the ability to make seed, large numbers of individuals result from vegetative multiplication. Some plants, especially among cultivated sorts, have entirely lost the ability to make seed and must be propagated by some asexual means. The banana, navel

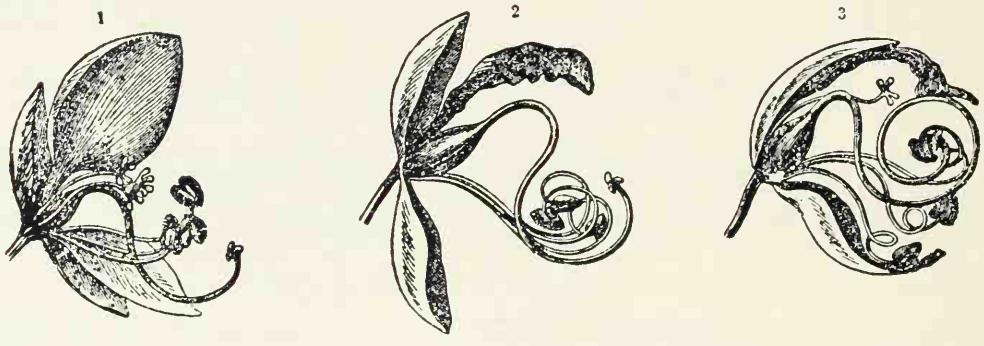


FIG. 16.—Adaptation for self-pollination by means of spiral twistings of stamens and style. (After Kerner.)

orange, seedless grape, and some varieties of the common potato are illustrations.

The purpose of sexual reproduction.—For the purpose of perpetuating the species or of increasing its numbers sexual reproduction, by the fusion of two individual organisms, does not seem to have any advantage over the vegetative method, self-perpetuation, which has just been noticed. In many forms of plant life, self-fertilization is not only possible but the rule. Wheat, rice, oats, and barley are seldom cross-fertilized. Tomatoes, peas, and beans likewise usually develop seed after fertilization with their own pollen.

Seed formation with and without pollination.—Curiously indeed, some plants that grow from seeds are not fertilized

at all. Seed develops freely on such plants when pollen is excluded. The dandelion propagates itself in this way, and no one would consider this intruder to be lacking in vigor or tenacity to life. A seed that develops without being fertilized is functionally merely a spore. It retains its complicated seed structure for the carrying of the embryo and storing of food for its use, but it is simply a special part of the plant set apart for reproduction. It is apparently a total abandonment of any advantage which sexual reproduction secured. On the other hand, we find

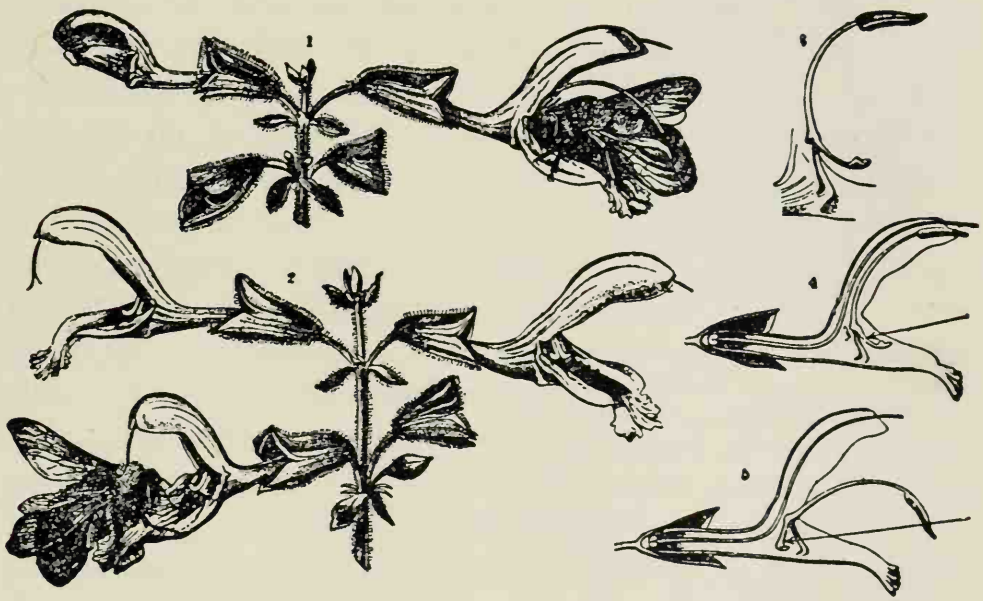


FIG. 17.—Adaptation for cross-pollination, transference of pollen by insects. (After Kerner.)

in many species intricate arrangements to prevent self-fertilization and to secure the union of different individuals. In some plants the two sexes can not function together, so that self-fertilization is impossible or rare. This is brought about in various ways: in some plants the stamens and pistils mature at different times; in others there are mechanical hindrances which prevent pollen from reaching the stigmas of the plant on which it was formed, while favoring its deposition on the stigmas of other plants of the same species; in some cases physiological incompatibility

makes it impossible for the pollen to grow on the stigmas of the same plant. As a matter of economy, it would seem to be to the advantage of plants to dispense entirely with cross-fertilization and even with pollen formation. The self-fertilized wheat plant is more certain to produce seed than the open-pollinated corn plant, as every one knows who has observed isolated corn plants and the resulting almost barren ears. The dandelion is even better off in this respect than wheat, because it is not obliged to expend energy and food in the manufacture of pollen. One seldom gives thought to the enormous production and wide distribution of pollen. An ordinary-sized corn plant, it has been estimated, makes more than 7,000,000 grains of pollen. Only about 500 of these are needed to produce an ear of grain. Other plants are even more prodigal in their lavish manufacture of pollen. Conifers throw out quantities of it, which are carried by the wind for hundreds of miles. It is even considered that certain deposits of coal were formed almost entirely from pollen of extinct plants. Surely, in this costly production and distribution of the male germ cells and the whole intricate mechanism of sex, some great purpose must be served.

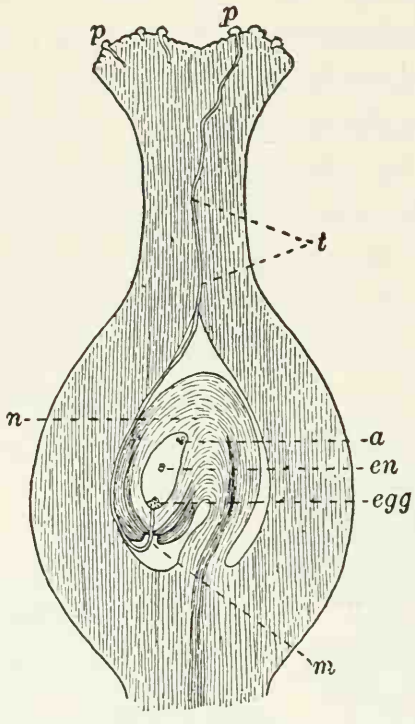


FIG. 18.—Diagram showing the process of sexual fertilization in the higher seed plants. Within the cavity of the ovary is an ovule (*n*), and within the ovule is an embryo sac. At the free end of the ovule is the micropyle (*m*). In the end of the embryo sac near the micropyle is the egg (*egg*) with two other nuclei lying close to it; in the center of the sac is the endosperm nucleus (*en*); and at the other end are the antipodal nuclei (*a*). Pollen grains (*p*) are on the stigma, and extending from one is shown a pollen tube which has grown down to the egg. (After Bergen and Caldwell in "Practical Botany," courtesy, Ginn & Co.)

Value of sexual reproduction.—It is not desirable here to enter into a full discussion of the biological significance of sexual reproduction. Its interest for the plant and animal improver lies in the connection it has with hybridization and the effects of inbreeding. The chief value of sex in this regard is in the creation of a far greater diversity of form and function than is possible with asexual reproduction. This greater variability enables the organism to adapt itself more quickly to a changing environment. It is also the dissimilarity made possible by this mode of reproduction which has enabled man to mold plant and animal life to fit his own needs.

Variability due to bisexual reproduction.—The greater diversity made possible by union of different individuals comes about in the following way: If an asexually propagated plant produces two new variations by some internal, germinal change at different intervals, and these variations persist in the offspring, three varieties of this plant then exist, the original form and the two variants. If this species is also able to reproduce seminally, it is possible, by crossing, to have still another form without any additional germinal variation. To state the matter more definitely, let us designate the first variation as A and the second as B. Now by crossing it is possible to bring the two together in the combination AB. Without sexual reproduction this form is not obtained unless both variations occur in the same individual, and this rarely happens. There are thus three different sorts in addition to the original type. When another variation C occurs, the possibilities are greatly increased. There are now the combinations AB, AC, BC, and ABC which can be formed, as well as the single variants A, B, and C, together with the original type. Only the last four could be brought about by asexual reproduction alone. When recombination can take place, as in this case, twice as many new forms can be easily created as when rearrangement is not possible. This advantage increases in an ever-growing magnitude as the number of original

variations becomes larger. N variations in asexual reproduction are simply n types, but the same number of changes in sexual reproduction make possible 2^n new forms. The variability increases not according to the number of germinal variations but as a progressive series. Since original hereditary variations are relatively infrequent in their occurrence, the immense advantage which sexual reproduction gives an organism in its struggle for existence is clearly apparent, and this process has been a vital factor in evolu-

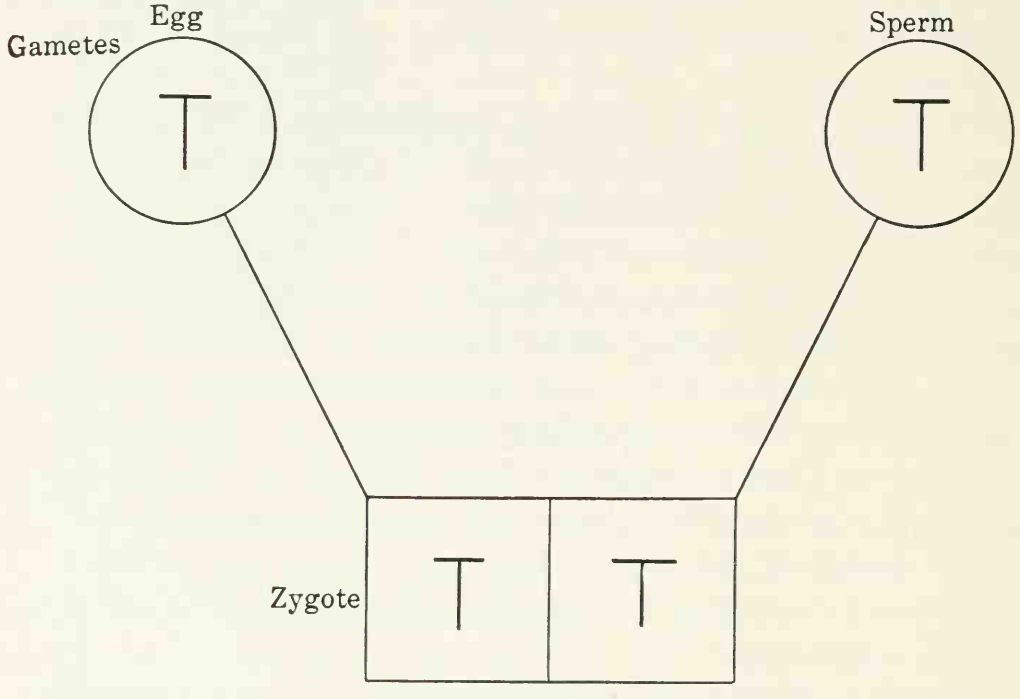


FIG. 19.—Diagram showing the union of gametes to form the zygote.

tion. It is equally important in plant and animal improvement, as it gives the originator of new forms a means of inducing plasticity, out of which there is the possibility of obtaining new types of value. The way in which variations are rearranged and handed on from one generation to another is briefly as follows:

The common garden tomato has two general types of plants in respect to their manner of growth. One of these is tall, with slender, rambling stems and smooth foliage. Plants of this type are called standard or tall plants, to

distinguish them from the dwarfs, which are short and stocky in habit of growth, with stiff stems and compact wrinkled leaves. When an ordinary tall tomato comes to produce seed, the pollen grain carries a height determiner or a **factor** which we may designate as T, which causes the plant to grow tall. The ovule likewise carries a similar **factor.** When the egg and sperm fuse, the two equivalent

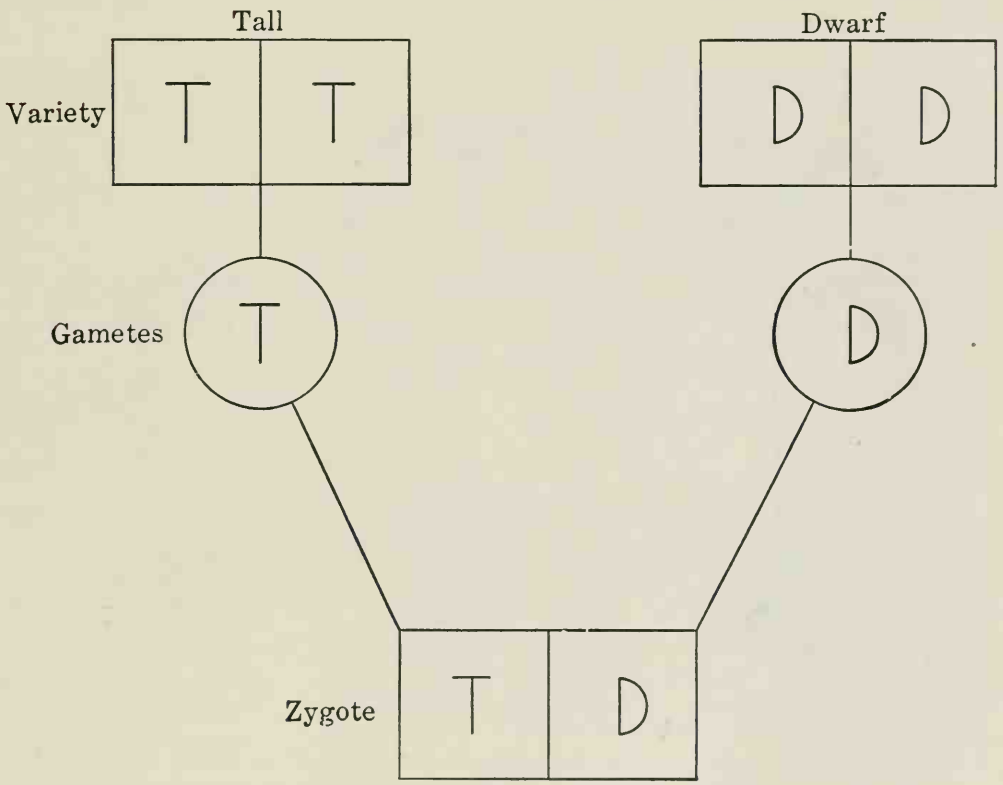


FIG. 20.—Diagram showing the union of unlike gametes to form a heterozygote.

factors are brought together. This procedure may be diagrammed as shown in Fig. 19.

The germs especially prepared for reproduction are called the **gametes**, and the product of their fusion the **zygote.** The latter grows into the adult, which in this case will be a tall tomato plant. As long as self-fertilization occurs, this variety will remain tall. The gametes all carry the same kind of determiner, so that there is no possibility of changing the type of growth unless some unforeseen alteration in the

factor itself takes place. When a tall plant is crossed by a dwarf variety the result is different as shown in Fig. 20. Here the gametes are unlike in regard to the factor for height, and all the cells of the resulting hybrid plant will carry the two different determiners. In this particular cross the hybrid is always tall like the standard parent, and usually it is impossible to distinguish between a pure tall plant and a hybrid tall plant. But when the crossed

FIG. 21.—The result, in the immediately following generation, of crossing a standard tomato plant (left) with a dwarf (right).

individual comes to reproduce in its turn, two kinds of gametes are formed, both in the eggs and in the sperm, one carrying T and the other D. These will be formed in in equal numbers.

When, therefore, this plant is self-fertilized, four combinations are possible:

T egg fertilized by T sperm gives TT, a tall plant.
T egg fertilized by D sperm gives TD, a tall plant.
D egg fertilized by T sperm gives DT, a tall plant.
D egg fertilized by D sperm gives DD, a dwarf plant.

The two reciprocal combinations of D and T are alike, as it makes no difference in this case whether the factor comes from the maternal or paternal side. It is important to note that while the TT and TD combinations look alike they will behave differently in future generations. The offspring in this second generation after the cross are visibly of two kinds, tall and dwarf. Some of the tall plants are **homozygous,** that is, the zygote is formed of like elements

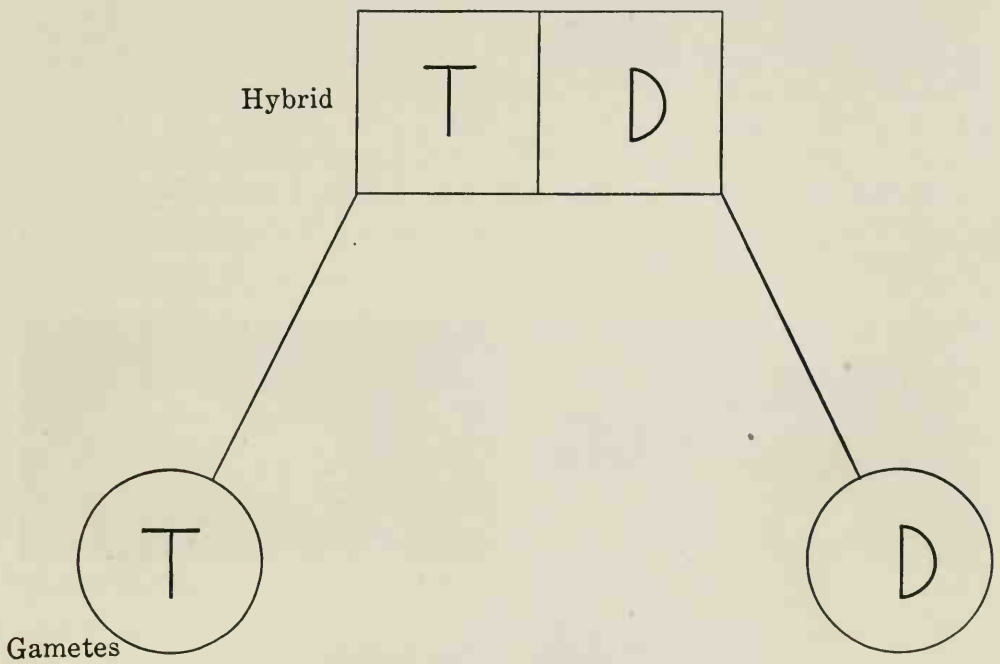


FIG. 22.—Diagram showing the production of two different kinds of gametes by a hybrid.

and will breed true like the original tall parent. Others are **heterozygous,** or hybrid, like their immediate parent and will again give the two kinds of offspring. The dwarf plants, however, being pure, or **homozygous,** for the dwarfing factor, will always remain true to that type as long as they are self-fertilized or crossed with only dwarf plants.

This method of distribution and transmission of character determiners is the same for animals. A white female guinea pig crossed by a black male, or the reverse combination, gives in either case black offspring. The sex-cells of

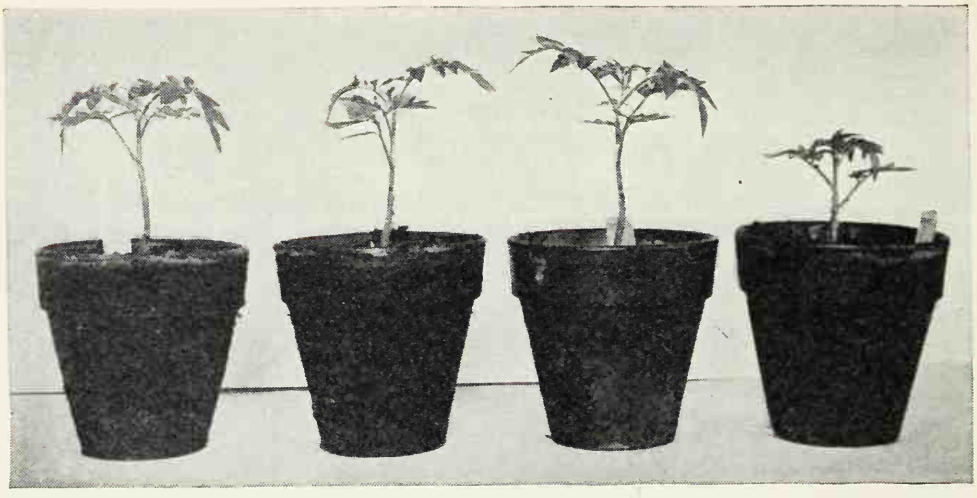


FIG. 23.—The progeny of the hybrid tomato plant shown in Fig. 21. Two out of every three tall plants in this second generation will, on the average, be hybrid like their parent and will again split up. One out of three will give only tall plants thereafter; and the one dwarf plant will always breed true for short stature.

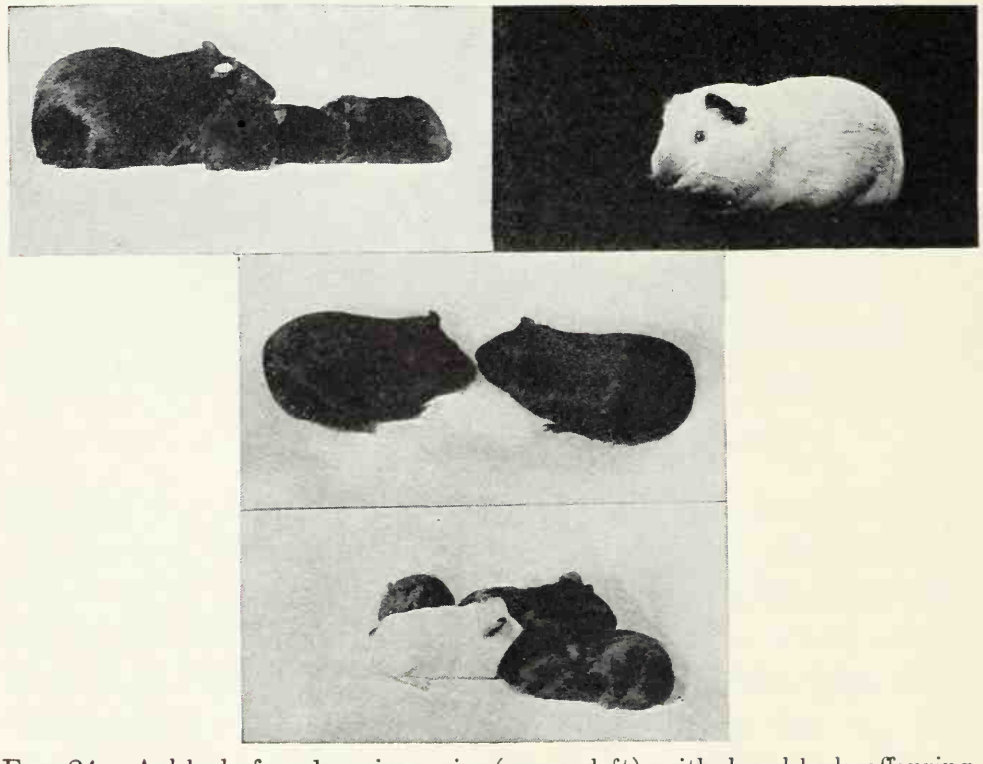


FIG. 24.—A black female guinea pig (upper left) with her black offspring by a white male (upper right). Two of these black offspring mated (center) give the black and white individuals shown (below), in the ratio of three black to one white. (After Castle in "Genetics and Eugenics," courtesy, Harvard University Press.)

such a hybrid are of two kinds—one determining white coat color, the other black. When a white-carrying egg is fertilized by a white-carrying sperm a white animal is produced, which as far as color is concerned is an exact reproduction of the grandparental pattern. All the other combinations are black; but some are pure black and will breed true to that color, while others are hybrid black and will produce some white offspring in later generations.

Recombination of hereditary factors.—In this way the inheritance is transmitted in sexual reproduction. No new forms have been created in these instances. The hybrid merely resembles one parent, and its offspring return to the two original grandparental types. But if, instead of crossing two tomatoes which are differentiated by a single character, we cross varieties differing in two ways, new combinations can then be formed. In addition to habit of vine, let us take color of fruit. A tall, yellow-fruited tomato is crossed with a dwarf, red variety. The immediate result is a tall plant, but with red fruit instead of yellow. Red color in the tomato masks yellow color, as tallness prevails over dwarfness. The hybrid differs from either parent, having received visible characters from both. When the gametes are formed, the factors for vine habit and fruit color are transmitted independently of each other, so that in the hybrid offspring there are four visibly different types having different combinations of the two contrasted characters, as follows:

Tall growth with yellow fruit.	Parental combination.
Dwarf growth with red fruit.	Parental combination.
Tall growth with red fruit.	New combination.
Dwarf growth with yellow fruit.	New combination.

All of these groupings of factors can be secured in a pure-breeding homozygous state, and therefore two new varieties of tomatoes, which are different from the two from which they came, have been established.

It is in this way that sexual reproduction operates to produce new forms. A third character can be added to all

these different combinations, making eight diverse kinds of tomatoes. A fourth would make sixteen different sorts, and so on until with ten characters over one thousand different varieties are possible. Without sexual reproduction there would be only ten. The significance of sexual reproduction, as contrasted with vegetative propagation in regard to the increased variability, is thus apparent.

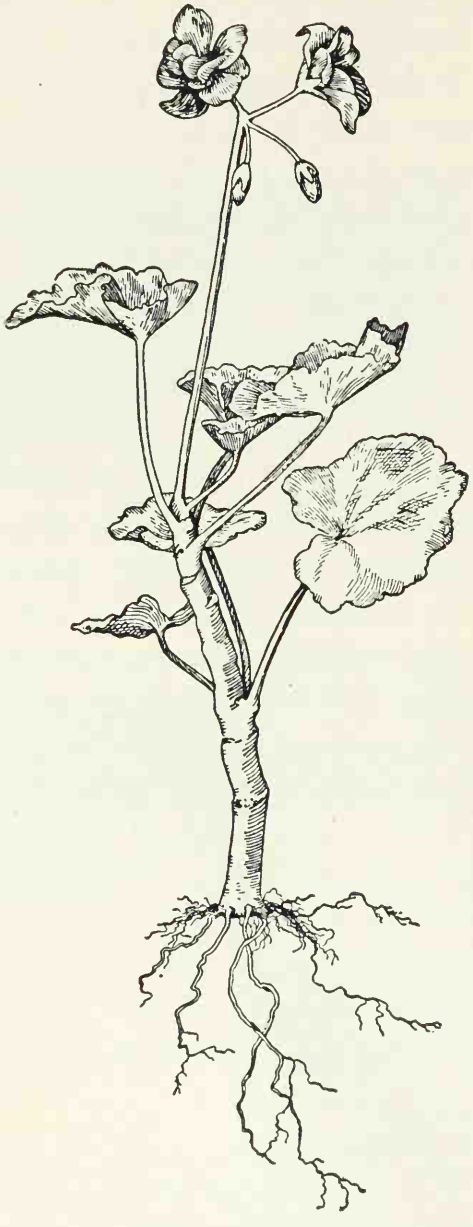


FIG. 25.—Vegetative reproduction by cuttings does not permit germinal recombination, so that a variety propagated in this way comes true to type whether it is heterozygous or homozygous. (After Bergen and Caldwell in "Practical Botany," courtesy, Ginn & Co.)

Vegetative propagation prevents recombination.—The difference between the two modes of multiplication is important. If a hybrid plant is propagated by any vegetative means, such as by cuttings, buds, grafts, or any other of the many means utilized for this purpose, the character of the plant remains the same throughout any number of such asexual generations. If the red-fruited, standard tomato resulting from the cross-pollination just mentioned is multiplied by cuttings (which is not the customary practice with this plant but can be easily done), the tall habit of vine and red color of fruit continue as constant features as long as the plants are

propagated in this manner. Dwarf plants or yellow fruit do not show up. There is no breaking up into the new and old combinations, as when seeds from this hybrid are planted. But no matter how many generations of vegetative cycles have intervened, when seed from such a hybrid is used for propagation, the hidden characters reappear and new arrangements of the various factors will be produced. When uniformity is desired, it is therefore very easily secured by vegetative propagation whenever this method can be employed. Most of the cultivated fruits and flowers reproduced in this way are hybrids of various degrees of complexity, carrying many characters hidden from sight in a heterozygous condition.

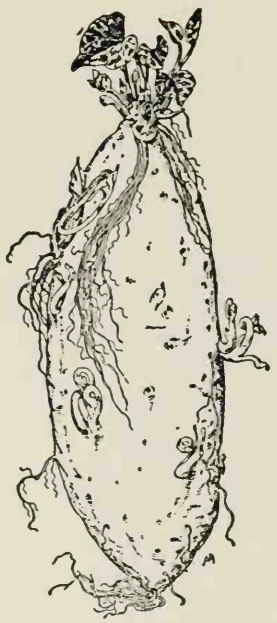


FIG. 26.—The use of sprouts from the roots, as in the sweet potato, is another method of propagation that insures fixity of type. (After Bergen and Caldwell in "Practical Botany," courtesy, Ginn & Co.)

Hereditary factors in development.—How the substances carried in minute quantities in the gametes can produce a given effect in different parts of the body of the mature organism is far from being clearly understood. It is evident that all of the hereditary factors, or determiners, are normally contained in all parts of the body. In some manner not yet understood, each determiner, in conjunction with other determiners and under suitable conditions, has the power to regulate growth in certain directions and produce the distinguishing features of the animal or plant. There is an interaction and coordination between all the organs of the body. Certain parts control the growth of other parts. Thus the growing tip of many plants has the power to suppress the lateral branches, but when the leader is accidentally destroyed one or more of the lateral branches take its place. Certain parts, when removed from the

influence of the remainder of the body, have the power of reforming the entire organism, as is commonly seen in asexual propagation. The gametes in sexual reproduction are specialized parts which have the power of throwing off the control of the remaining parts of the individual and

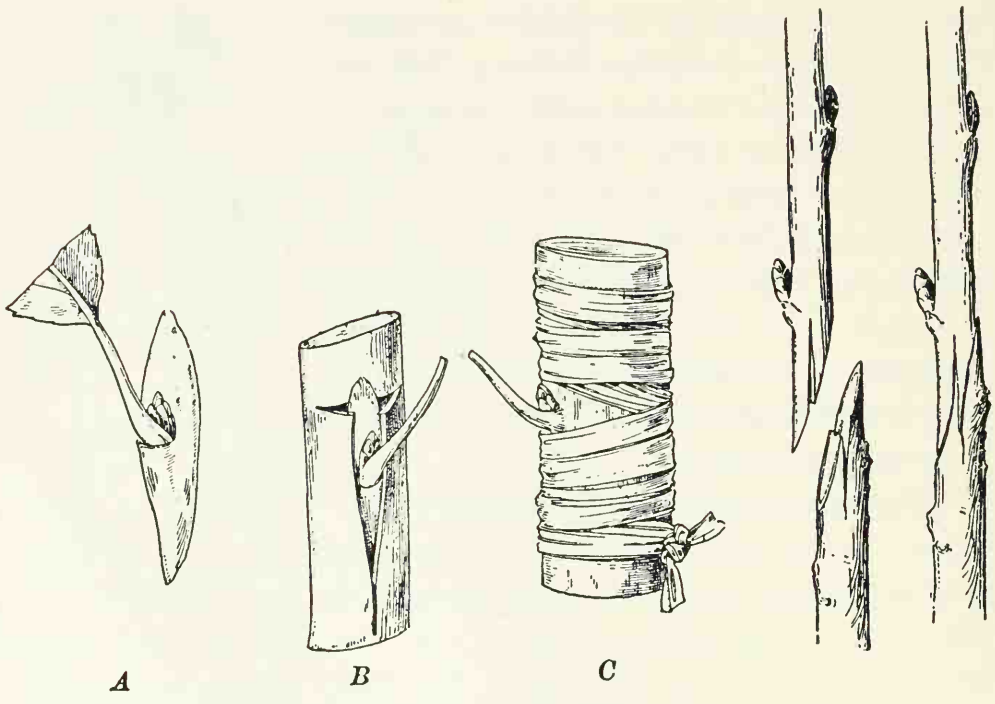


FIG. 27.—Propagation by budding or grafting brings about uniformity in the cion; but unless the root stocks are also propagated vegetatively they will show the usual seedling variation. (After Bergen and Caldwell in "Practicaly Botany," courtesy, Ginn & Co.)

leading a more and more independent existence until complete separation from the parent is effected.

Summary.—The primary importance of sexual reproduction, therefore, lies in the fact that it produces greater variability, making possible an increased elasticity in adaptiveness to new and varied surroundings. This has the greatest value for the plant or animal improver, because, by proper crossing, he can create variations, which will be the basis for new forms of value. Asexual reproduction maintains uniformity. This is usually highly desirable in

cultivated plants, and whenever vegetative propagation can be successfully practiced this means of multiplying plants is generally utilized. Some valuable plants propagated in this way no longer retain the ability to make seed, and their further improvement is therefore difficult.

CHAPTER IV

SEGREGATION AND RECOMBINATION

The first artificial hybrid upon record is credited to Camerarius, who described, in 1694, the effect of crossing the hemp with the hop. Thomas Fairchild, in 1717, pollinated a carnation by a pink and from this resulted a variety known as Fairchild's Sweet William, which was grown for many years afterwards. Linnaeus, the famous Swedish taxonomist, about the same time crossed two species of salsify to prove that a new plant, which he had found growing in the wild, was a natural hybrid between these two forms. It was not until the time of Kölreuter, however, in 1760, that extensive hybridization experiments were performed. By many crosses among different species of tobacco and of other plants, Kölreuter proved that a hybrid progeny, made by cross-pollinating two pure types, was as uniform as either of the parents in the first generation after crossing, and generally partook of features of both. In the following generation the hybrid broke up into diverse types, some of which returned to the type of one or the other parent.

In the century that followed, many investigators gave almost their entire time to experimental crossing. In addition to the facts which Kölreuter established, it was noted that many characters disappeared from sight in the hybrids but reappeared in later generations. This had long been known to animal breeders. The ability of sires to suppress undesirable features in the animals with which they were mated, called prepotency, was a very valuable characteristic and was greatly sought for. But notwithstanding the effort expended in experimental work with plants and the many centuries in which animal breeding had been intensively

practiced, little more was known about heredity than the few facts outlined. No experiments were carried out in such a way as to make it possible to predict the character of the hybrid in any particular case, or the different forms in which the offspring of a hybrid would appear, or their relative numbers. Truly did Balzac write that, "Heredity is a sort of maze in which science loses itself."

Mendel's experiments with the garden pea.—About the time that this just accusation was being made, Johann Mendel (1822–1884), renamed Father Gregor when he was admitted to the Augustinian Order in the Monastery at Brünn, Austria, conducted a well-planned and carefully executed series of experiments on heredity in plants. Mendel set before himself the task of following individual characters from one generation to another and the behavior of several of these characters in relation to each other. He had noted that there were many differences in peas, such as tall and dwarf stems, wrinkled and smooth seeds, colored and uncolored seeds, and other features. He crossed plants having such contrasted characters, recorded the nature and number of the progeny from these self-fertilized hybrids during many years, and, in 1866, published his observations in a journal of the local natural history society. Although this publication was received at many libraries in Europe and America, his treatise, which contained the key to many problems which were widely discussed in his time, attracted no attention. The results of his experiments, which were clearly and concisely stated and explained by him, and which were destined to have such far-reaching consequences that they may be considered as the beginning of the science of genetics, were ignored, or unknown, for nearly fifty years, until several investigators, working along the same lines and independently, arriving at the same conclusions as had Mendel, discovered his article in 1900. The influence of Mendel's work, therefore, begins at the opening of the present century instead of at the time of its publication.

Mendel's discovery.—The basic principle of the method of inheritance made clear by Mendel has been outlined in the previous chapter. Let us now examine his conclusions more closely. For this purpose another illustration will be chosen. Varieties of the Adzuki bean have two kinds of seed coats: one is uniformly light colored; the other is

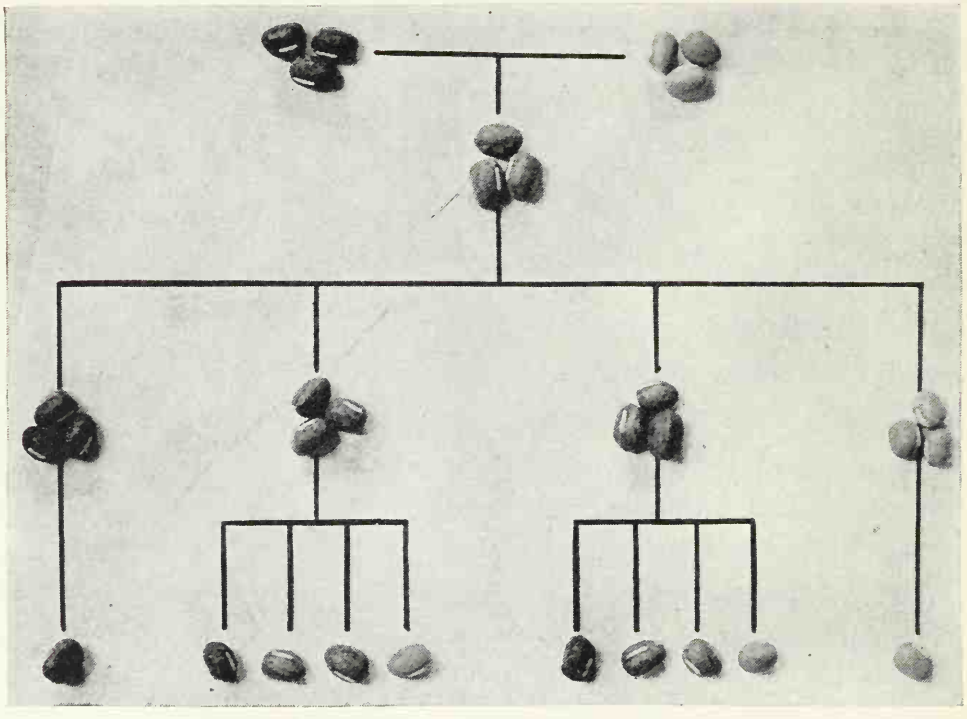


FIG. 28.—Dark mottled and self-colored beans, when crossed, give plants in the first following generation which produce light mottled seeds distinct from either parental type. These hybrid seeds give in the second generation three distinct classes of plants in the ratio of 1 · 2 : 1, having either mottled, light mottled, or self-colored seeds. The dark mottled and self-colored seeds, which reduplicate the two grand parental types, breed true from then on, while the light mottled seeds in every generation thereafter break up into the three classes and in the ratio of 1 : 2 : 1. (After Blakeslee in Jour. Heredity.)

mottled. When these two types are crossed (Fig. 28), the hybrid progeny has seeds which are light mottled and can be distinguished from either parental type. When the hybrid seeds are planted, the resulting second generation has three different kinds of plants in respect to the color of the seed; dark mottled, light mottled, and uniformly colored. As in

the tomato illustration previously given, there is a return to the two grandparental types. In this case, however, the hybrid combination can be distinguished from either of its progenitors, but is mottled like one grandparent. The proportion in which these three different types appear is approximately the same every time the segregating generation is grown. They are in the ratio of *one* dark mottled, *two* light mottled, and *one* self-colored. The reason for this is as follows: The gametes which are produced for sexual reproduction are formed in equal numbers with respect to any single hereditary difference. In the process of fertilization, it is a matter of chance whether like gametes or unlike gametes unite. The mottling determiner, which prevails in this instance over the plain seed coat color, may be represented by the capital letter *M*, and the absence of mottling by the small letter *m*. *M* eggs may be fertilized by *M* or *m* sperm; *m* eggs may also be fertilized by *M* or *m* sperm. The result is as follows:

Egg	Sperm	Zygote		
M	*M*	*MM*	1 Dark mottled	3 Mottled
M	*m*	*Mm*	2 Light mottled	
m	*M*	*mM*		
m	*m*	*mm*	1 Self-colored	1 Unmottled

As the two heterozygous combinations are alike, the ratio is 1 : 2 : 1 of plants having dark mottled, light mottled, and self-colored seeds; and considering the color pattern alone the ratio is 3 : 1 of mottled and unmottled. The numbers realized in any particular case rarely agree exactly with this theoretical ratio, just as a tossing of pennies does not always give an equal number of heads and tails. But if a sufficiently large number of offspring are grown, the total numbers will agree closely with this ratio.

The dark mottled seeds recovered in the second generation will continue to breed true to that type, as will also the

self-colored seeds, as long as they are not again crossed. The light mottled seeds, however, since they are just like the original hybrid, will continue to break up in the same ratio of 1 : 2 : 1. This procedure may be diagrammed as follows:

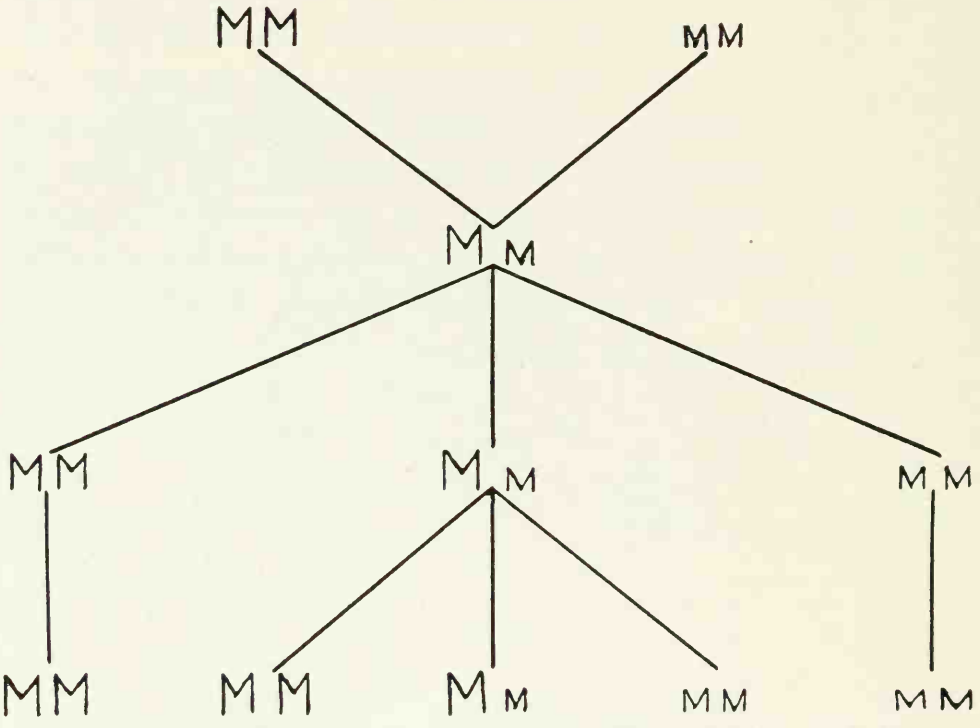


FIG. 29.—Diagram showing the genetic composition of dark mottled plants (*MM*) crossed with self-colored plants (*mm*) and of their progeny in the three following generations.

Dominant and recessive characters.—Because the mottling prevails over the unmottled condition whenever the two different determiners are present together, the mottling is spoken of as the **dominant** character and the absence of mottling as the **recessive.** In many cases the pure dominant and the hybrid dominant can not be distinguished, and therefore the ratio of types in a segregating progeny, like the tall and dwarf tomatoes or black and white guinea pigs, is 3 : 1 instead of 1 : 2 : 1. Other cases, in which at first sight one character is hidden from view completely, show on further examination that there has been an interaction of both members of the pair, so that dominance is not perfect.

Characters differ in this respect: with some, apparently complete dominance is the rule; others show a partial dominance or even a strictly intermediate condition. Usually, with a character like color, there is at least partial dominance. The color of one parent only is visible in the hybrid. Generally the darker color prevails over the lighter one, but frequently there is a dilution of color so that some effect of the hybrid union can be discerned. If a glass of ink is poured into a glass of water, the resulting mixture is black and to the eye it may have as deep a shade as the undiluted ink. The black and white coat of guinea pigs behaves in much this fashion. On the other hand, crossing yellow and white corn gives pale yellow seeds. Similarly, the cross of red and white four o'clocks gives a pink flower which is distinct from either parent type. Whether dominance is perfect or not, or even if there is no dominance, segregation and recombination occur, so that the original characters are restored in all their purity. It is the conception of the recombination of **unmodified** units which is the great contribution of Mendel to the study of heredity.

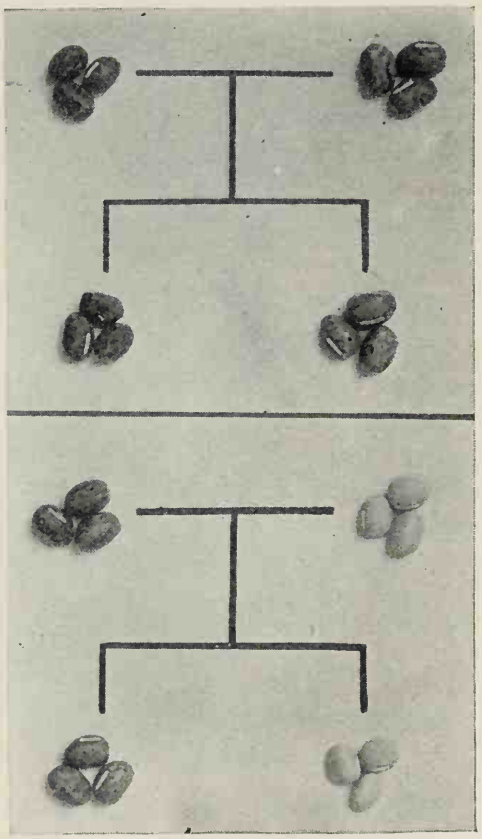


FIG. 30.—The result of back-crossing the hybrid with both parental types. Light mottled by dark mottled gives only these two classes in the offspring and in equal numbers. Similarly, the hybrid, light mottled type crossed by the recessive gives only light mottled and self-colored seeds in equal proportion. (After Blakeslee in Jour. Heredity.)

Back-crossing.—The fact that this hybrid produces two kinds of gametes is shown when it is back-crossed with either

parent. The cross may be made both ways; i.e., pollen from the hybrid may be placed on the stigmas of the parents or pollen from the parents used on the hybrid. The result of such back-crossing is shown in Fig. 30. Light mottled seeds crossed with dark mottled give plants with light and dark mottled seeds in equal numbers. In the same way, crossing the hybrid, light mottled, with self-colored plants gives light mottled and self-colored plants in equal numbers. The reason for these results is shown in Fig. 31.

Designating hybrid generations.—The first generation following the cross of two contrasted types, differing in one or more respects, is usually called the first filial generation,

FIG. 31.—Diagram showing the composition of the zygotes in back-crossing the hybrid type (*Mm*) with the dominant (*MM*) and with the recessive (*mm*).

or simply the F_1 as a short-hand notation. The second generation grown from seeds produced by F_1 plants is designated as F_2, and so on. Similarly, the parents are designated as P, the first ancestral generation being P_1, the grandparental generation P_2, etc.

Illustration of complete dominance.—In addition to the example of the tall and dwarf tomato, given previously, another common illustration of apparently complete dominance is found in corn. Sweet corn has characteristic wrinkled and translucent kernels, while ordinary field corn has smooth, opaque seeds. The difference is due to a single Mendelian determiner which allows the starch to develop in one case and not in the other. If an ear of sweet corn is fertilized with field corn pollen, all the kernels which

develop are starchy and the ear looks like ordinary field corn. If the pollination is made the other way there is no

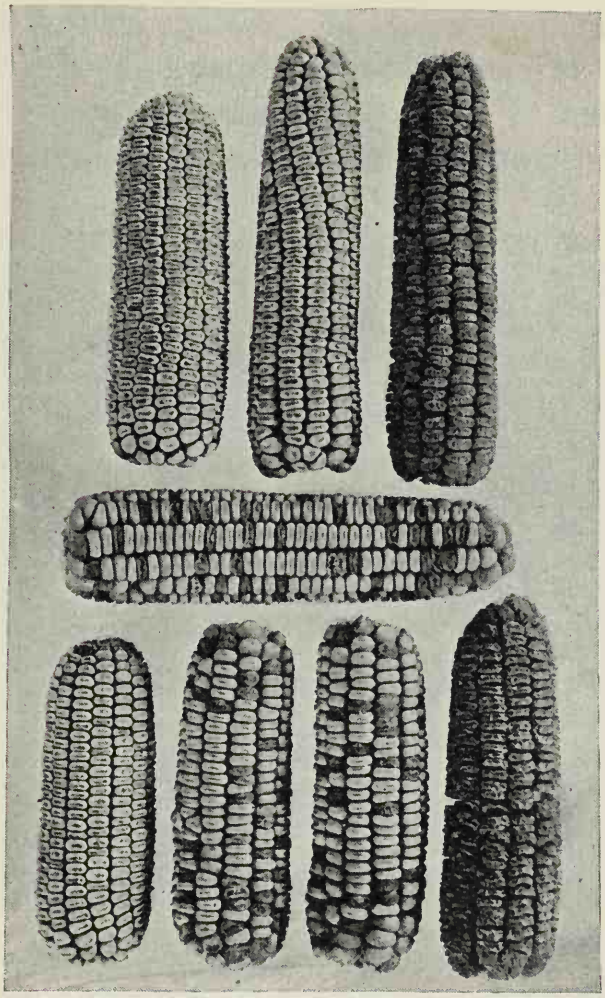


FIG. 32.—When sweet corn is pollinated by field corn, the immediately resulting seeds are smooth and opaque like field corn, as shown in the top row (center). The hybrid plants grown from these seeds when self-fertilized or inter-bred give segregating ears (middle) having three smooth, opaque seeds for every one that is wrinkled and translucent. The dominant starchy seeds give two classes of plants, those which breed true and those which segregate, while the recessive sweet seeds produce only wrinkled, translucent seeds when self-fertilized or pollinated with their own kind of pollen.

visible effect, because the starchy condition is always dominant and the ears therefore remain unchanged. But when either of these crossed seeds is planted and the resulting

ears self-pollinated or pollinated by similar hybrid plants, the sweet seeds reappear in the expected ratio of 3 starchy to 1 sweet.

The immediate effect of crossing upon some plants.—In the case of seed characters in corn, it should be noted that the effect of crossing is immediate, and is realized one year sooner than it would be with most plants, such as the

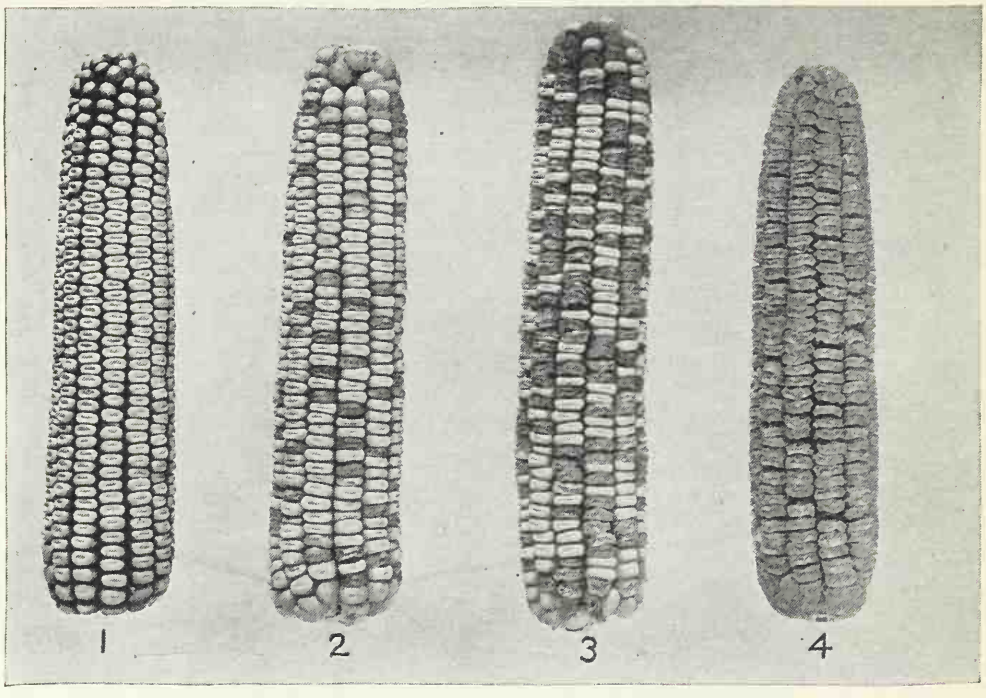


FIG. 33.—When the hybrid plants grown from the seeds from the cross-pollinated ear (1) are back-crossed with the recessive (4), the result (3) is starchy and sweet seeds in the ratio of 1 to 1 instead of the 3 to 1 ratio obtained in (2) when the hybrid plants are self-fertilized, showing that the two kinds of gametes are produced by the hybrid in equal numbers.

tomato and Adzuki bean. With corn, the F_1 seeds, borne on the parent plant, may be changed in form and color when dominant factors are brought in by the pollen. This effect is called **xenia** and is due to a special tissue in the seed, which is called the **endosperm** and consists of stored food produced for the nourishment of the growing embryonic plant. This tissue also develops by a fertilization process. A fused endosperm nucleus unites with a second male nu-

cleus, and fertilization takes place in much the same way that the embryo is formed. This process is called **double fertilization.** The cells which join to form the nutritive tissue always carry the same characters as the egg and sperm which unite to form the embryo. The appearance of the seed is therefore a guide to the determiners possessed by the seedling. Endosperm characters may be considered as seed characters which appear at the beginning of the plant's life cycle instead of at the close.

The green and yellow or the wrinkled and smooth seeds of peas are similar to corn in showing an immediate effect of cross-pollination. However, there is no endosperm tissue in the mature seed of peas, all the food being stored in the embryo. It is the color, or chemical nature, of this embryo, showing through the colorless seed coat, which reveals the character of the seeds. In both peas and corn this outer seed coat may also be colored, as in the case of the Adzuki beans; but this tissue belongs to the same generation as the parent plant and is not immediately affected by cross-pollination. When the outer coat of corn is colored the entire ear is colored, as in the familiar ears of red corn found in nearly every field. When ordinary white or yellow corn, in which the outer hull is uncolored, is crossed with red corn, the ears which develop from the pollination are not colored, but the plants grown from these crossed seeds will have red ears, and segregation in the next generation is between different plants and not between individual seeds on an ear.

The tranmission of two Mendelian units.—In the common varieties of both field and sweet corn, which may have either yellow or white seeds, yellow is dominant over white. The determiner which produces yellow will here be designated as *Y* and the absence of this color as *y*. Similarly, the starchy endosperm already described will be called *S*, and the alternate sweet condition *s*. When a yellow sweet corn variety with the composition *YYss* is crossed with a white starchy variety *yySS*, the resulting F_1 seeds

are all yellow and starchy and have the formula *YySs*. When these hybrid plants produce gametes, there will be four different kinds. These will be produced in equal numbers in the ovules and in the pollen grains and will have the composition *YS*, *Ys*, *yS*, or *ys*. It should be noted that each gamete can receive only one of the two contrasted determiners and never both. When such a plant is self-pollinated, the result can be best shown in the form of a checkerboard, where the pollen grains are represented on one side and the ovules along another, as in Fig. 34.

	YS	Ys	yS	ys
YS	YS YS yellow starchy	Ys YS yellow starchy	yS YS yellow starchy	ys YS yellow starchy
Ys	YS Ys yellow starchy	Ys Ys yellow sweet	yS Ys yellow starchy	ys Ys yellow sweet
yS	YS yS yellow starchy	Ys yS yellow starchy	yS yS white starchy	ys yS white starchy
ys	YS ys yellow starchy	Ys ys yellow sweet	yS ys white starchy	ys ys white sweet

FIG. 34.—Checkerboard showing the result in the second generation of crossing a yellow, sweet corn and a white, starchy variety. The composition of the gametes (pollen grains and ovules) is shown along the top and side, while each square indicates the composition of the different classes of zygotes obtained by the possible combinations of these gametes.

There are 16 squares in such a checkerboard, and the formula of the pollen grain is written above and of the ovule at the left of each column. The composition of all the different types of seeds obtained in F_2 is shown in the

squares. In every one in which *Y* appears the seed will be yellow. In every square where *S* appears the seed will be starchy. This will be so whether the capital letter is present once or twice, since both these characters show dominance. If the visibly different kinds of seeds are classified, it will be seen that there are four. These are: yellow starchy, yellow sweet, white starchy, and white sweet. Starting with only two original types, two new ones have been formed. The numbers of these four different kinds of seeds and their factorial composition, which will determine their behavior in later generations, are as shown in Table II.

TABLE II

THE THEORETICAL NUMBER OF INDIVIDUALS, AND THEIR COMPOSITION OBTAINED IN F_2 FROM A CROSS OF YELLOW, SWEET WITH WHITE, STARCHY CORN

Number of Individuals	Genotype Class	Phenotype Class	Ratio of of Phenotypes	Breeding Behavior
1	YYSS	Yellow starchy	9	Breeds true
2	YYSs			Segregates, starchy sweet, 3 : 1
2	YySS			Segregates, yellow white, 3 : 1
4	YySs			Segregates, yellow white, starchy sweet, 9 : 3 : 3 : 1
1	YYss	Yellow sweet	3	Breeds true
2	Yyss			Segregates yellow white, 3 : 1
1	yySS	White starchy	3	Breeds true
2	yySs			Segregates starchy sweet, 3 : 1
1	yyss	White sweet	1	Breeds true
16			16	

Individuals appear alike but breed differently.—The double recessive appears only once in every 16 times. It is noteworthy that many of the other seeds in F_2 look alike, but will behave differently in the following generations. For example, *YYSS* and *YySs* are both yellow and starchy; the former will breed true while the latter will not. *The*

only way to prove their composition is to grow the plants and examine their progenies. This is one of the most important contributions of Mendel to the knowledge of heredity. He

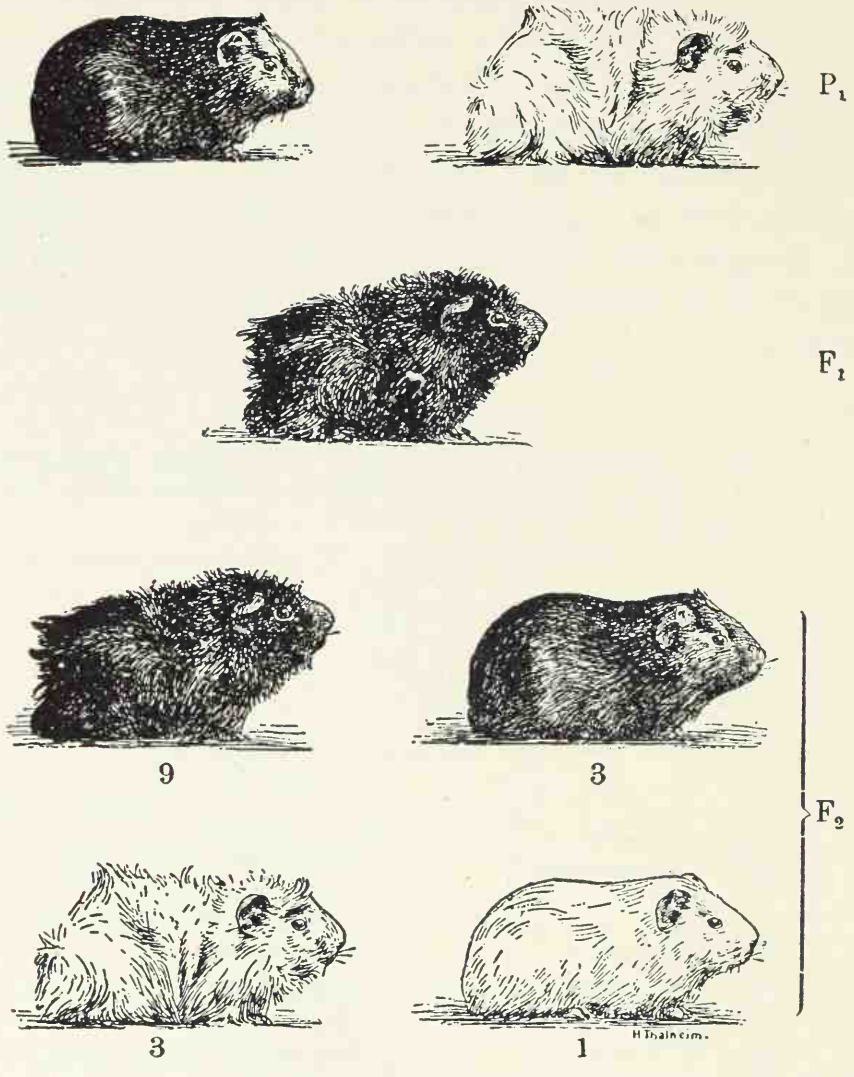


FIG. 35.—The result of crossing a smooth, black-haired with a rough, white-haired guinea-pig. Rough and black hair are dominant, and in F_2 the ratio is 9 rough black : 3 smooth black : 3 rough white : 1 smooth white. (After Baur from Babcock and Clausen's "Genetics in Relation to Agriculture," courtesy, McGraw–Hill Book Co.)

was the first to show clearly that the hereditary composition of any individual can only be determined positively from its progeny and not by its appearance.

Similar behavior of unit characters in transmission

holds true for animals as well as plants. For example, the result of crossing a black guinea pig with smooth hair with a white, rough-haired animal is a first-generation progeny all of which are black with rough hair. In the following generation the four combinations—black rough, black smooth, white rough, and white smooth—are obtained in the dihybrid ratio of 9 : 3 : 3 : 1, as shown in Fig. 35.

Mendel's principles of heredity.—With these examples in mind, the principles of Mendelian heredity may now be stated in general terms. Transmissible determiners, which govern the development of characters, segregate in the formation of the reproductive cells and recombine according to chance allotment to form the subsequent generations. This, stated in various ways, is generally known as Mendel's Law of Heredity. There are involved in this statement, however, two important rules, as follows:

1. *The law of segregation.*—Determiners which govern character development are unmodified by others with which they are brought into contact during the lifetime of any particular individual. The characters transmitted from generation to generation have their basis in a number of definite entities, each with an individuality of its own, and each is handed on uninfluenced by the organism in which it dwells. Each unit character in the individual is represented twice in the fertilized egg and the cells which grow out of it, once in the hereditary allotment received from the mother and once in that received from the father. These paired determiners separate in the formation of germ cells, so that when the two members of any pair differ the gametes are unlike.

2. *The law of recombination.*—The units carried by the different chromosomes are shuffled about and put in all possible combinations, according to chance. As each determiner is transmitted independently, of the others, the particular set of factors which went into the hybrid from either of the two parents is restored in only a small proportion of the F_2 individuals, according to the number of differences involved.

If there is only one pair in which segregation is occurring, the parental combination is returned once in every four individuals on the average; with two pairs, once in every sixteen, and with three pairs, once in sixty-four individuals, and so on. The remaining numbers form new combinations made up of maternal and paternal characters in varying proportions.

The generality of Mendel's principles.—In the two decades which have elapsed since the rediscovery of Mendel's principles of heredity, the generality of his laws has been confirmed by an ever-increasing number of experiments with many different forms of animals and plants. The doctrine of segregation and recombination of unit factors has been found to hold true for nearly all the domesticated animals, and in addition to these, mice, rats, guinea pigs, fishes, flies, moths, beetles, and snails. Nearly all of the common field crops and garden flowers, as well as many wild species, have given unmistakable evidence of these processes in inheritance. Segregation and recombination of hereditary units is the basis on which heredity is now studied. That the hypothetical determiner is never modified by the alternate members of the pair with which it is associated while in hybrid union, or by the individual in which it resides, has been disputed. It is not necessary to review here the evidence for or against this position. Cases of such modification or contamination of determiners have not been clearly established. They are practically all found in material in which the hereditary situation is not thoroughly known. The possibility of such an effect can not be denied, but if there is any it is so small and occurs so seldom that it can not have any real significance for the practical improvement of animals and plants. Organisms, heterozygous for various factors, have been kept in that condition for many generations with no visible effect upon the recessive characters, which have remained hidden all the time.

Hereditary determiners uninfluenced by each other.—An illustration is furnished by a farmer in Connecticut who

has been growing a kind of flint corn in which all the ears have a mixture of yellow and white seeds. Obviously, such ears resulted originally from a cross of yellow and white corn. This corn has been grown by the family for over sixty years. Someone had taken a fancy to such variegated ears and had always selected them for seed, naming the variety Pied Flint. For all these years, Mendelian combination and segregation of yellow and white color has been going on, but the colors now differ in no way from the ordinary yellow and white of commonly grown pure varieties of flint corn. One can not hope, therefore, to make a standard tomato smaller in growth by crossing it with a dwarf tomato. It is possible to have either a standard or a dwarf tomato, as desired, but new types intermediate in habit of growth between the two are not to be looked for in a blending of these separate determiners, as the experimental evidence shows that such an interaction does not take place. Variations in the expression of characters are continually ocurring, particularly where crossing is frequent; but all evidence goes to show that these variations are due to different combinations of hereditary determiners and modifying factors and not to alterations of the individual determiners themselves.

The trihybrid.—The manner in which Mendelism works with one and with two character pairs has already been shown. The same principle holds for any number of such alternative differences, but the complexity increases greatly as the number of determiners grows larger. In addition to the two characters in corn already used, a third will be employed, the determiner *P*, which produces purple in the aleurone layer of corn. This color is familiar in the Black Mexican sweet corn, and numerous varieties of corn cultivated by the Indians. The purple color, which becomes black on maturity, is situated in a thin layer called the **aleurone** at the outside of the endosperm tissue and just underneath the outer hull or pericarp. The color in certain crosses behaves as a simple Mendelian difference with

	PYS	PYs	PyS	pYS	Pys	pYs	pyS	pys
PYS	PYS PYS purple yellow starchy	PYs PYS purple yellow starchy	PyS PYS purple yellow starchy	pYS PYS purple yellow starchy	Pys PYS purple yellow starchy	pYs PYS purple yellow starchy	pyS PYS purple yellow starchy	pys PYS purple yellow starchy
PYs	PYS PYs purple yellow starchy	PYs PYs purple yellow sweet	PyS PYs purple yellow starchy	pYS PYs purple yellow starchy	Pys PYs purple yellow sweet	pYs PYs purple yellow sweet	pyS PYs purple yellow starchy	pys PYs purple yellow sweet
PyS	PYS PyS purple yellow starchy	PYs PyS purple yellow starchy	PyS PyS purple white starchy	pYS PyS purple yellow starchy	Pys PyS purple white starchy	pYs PyS purple yellow starchy	pyS PyS purple white starchy	pys PyS purple white starchy
pYS	PYS pYS purple yellow starchy	PYs pYS purple yellow starchy	PyS pYS purple yellow starchy	pYS pYS white yellow starchy	Pys pYS purple yellow starchy	pYs pYS white yellow starchy	pyS pYS white yellow starchy	pys pYS white yellow starchy
Pys	PYS Pys purple yellow starchy	PYs Pys purple yellow sweet	PyS Pys purple white starchy	pYS Pys purple yellow starchy	Pys Pys purple white sweet	pYs Pys purple yellow sweet	pyS Pys purple white starchy	pys Pys purple white sweet
pYs	PYS pYs purple yellow starchy	PYs pYs purple yellow sweet	PyS pYs purple yellow starchy	pYS pYs white yellow starchy	Pys pYs purple yellow sweet	pYs pYs white yellow sweet	pyS pYs white yellow starchy	pys pYs white yellow sweet
pyS	PYS pyS purple yellow starchy	PYs pyS purple yellow starchy	PyS pyS purple white starchy	pYS pyS white yellow starchy	Pys pyS purple white starchy	pYs pyS white yellow starchy	pyS pyS white white starchy	pys pyS white white starchy
pys	PYS pys purple yellow starchy	PYs pys purple yellow sweet	PyS pys purple white starchy	pYS pys white yellow starchy	Pys pys purple white sweet	pYs pys white yellow sweet	pyS pys white white starchy	pys pys white white sweet

FIG. 36.—Checkerboard showing the recombinations possible in F_2 from a cross of purple, yellow, starchy corn (*PP YY SS*) with non-purple, white, sweet corn.

TABLE III

THE THEORETICAL NUMBER OF INDIVIDUALS, AND THEIR COMPOSITION, OBTAINED IN F_2 FROM A CROSS OF PURPLE, YELLOW, STARCHY CORN WITH A NON-PURPLE, WHITE, SWEET VARIETY

Number of Individuals	Genotype Class	Phenotype Class	Ratio of Phenotypes	Breeding Behavior
1	PPYYSS	Purple yellow starchy	27	Breeds true
2	PpYYSS			Segregates purple white, 3 : 1
2	PPYySS			Segregates yellow white, 3 : 1
2	PPYYSs			Segregates starchy sweet, 3 : 1
4	PpYySS			Segregates purple white, yellow white, 9 : 3 : 3 : 1
4	PPYySs			Segregates yellow white, starchy sweet, 9 : 3 : 3 : 1
4	PpYYSs			Segregates purple white, starchy sweet, 9 : 3 : 3 : 1
8	PpYySs			Segregates purple white, yellow white, starchy sweet, 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1
1	PPYYss	Purple yellow sweet	9	Breeds true
2	PPYyss			Segregates yellow white, 3 : 1
2	PpYYss			Segregates purple white, 3 : 1
4	PpYyss			Segregates purple white, yellow, white, 9 : 3 : 3 : 1
1	PPyySS	Purple white starchy	9	Breeds true
2	PPyySs			Segregates starchy sweet, 3 : 1
2	PpyySS			Segregates purple white, 3 : 1
4	PpyySs			Segregates purple white, starchy sweet, 9 : 3 : 3 : 1
1	ppYYSS	White yellow starchy	9	Breeds true
2	ppYySS			Segregates yellow white, 3 : 1
2	ppYYSs			Segregates starchy sweet, 3 : 1
4	ppYySs			Segregates yellow white, starchy sweet, 9 : 3 : 3 : 1
1	ppyySS	White white starchy	3	Breeds true
2	ppyySs			Segregates starchy sweet, 3 : 1
1	ppYYss	White yellow sweet	3	Breeds true
2	ppYyss			Segregates yellow white, 3 : 1
1	PPyyss	Purple white sweet	3	Breeds true
2	Ppyyss			Segregates purple white, 3 : 1
1	ppyyss	White white sweet	1	Breeds true
64			64	

dominance of color in F_1 and segregation into purple and white seeds in F_2 in the usual 3 to 1 fashion. When a purple, yellow, starchy variety, *PP YY SS*, is crossed with a non-purple, white, sweet variety, *pp yy ss*, the F_1 seeds are all colored and starchy. It is necessary to cut through the outer purple layer to see the yellow endosperm underneath. The different kinds of seeds obtained on self-fertilized F_2 ears, and their composition, are found most easily by the checkerboard system. Eight different kinds of gametes are produced, making possible sixty-four different combina-

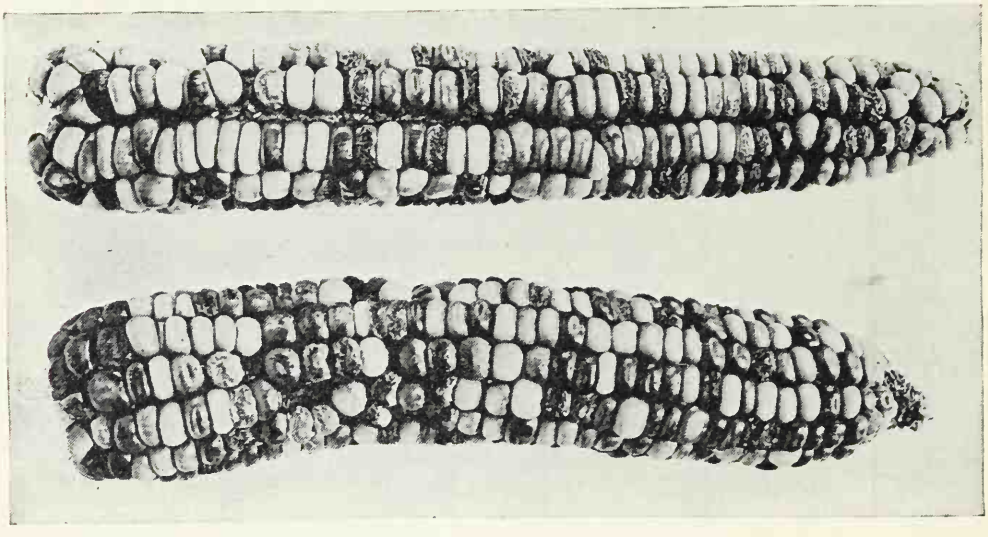


FIG. 37.—Self-fertilized F_2 ears from a cross of purple, yellow, starchy corn with a non-purple, white, sweet variety.

tions. As before, many of these combinations will look alike, but will behave differently in later generations, as shown in Fig. 36 and Table III.

To show how the results actually obtained agree with the theoretical expectation, the figures secured from two F_2 ears (shown in Fig. 37) of a cross involving these three factors are given in Table IV. The numbers from one ear agree very closely with the numbers expected. Those from the other are not so closely in accord with theory, but the figures as a whole show that there is recombination of all the charac-

ters involved and the numbers obtained are reasonably near the expected distribution. It is to be noted that in one case only one seed in a total of 136 had all three recessive characters. Theoretically, one in every 64 seeds should have this constitution. This brings out the fact that it is necessary to grow from two to three times as many individuals as theory calls for, in order to run a fair chance of getting all the possible combinations.

TABLE IV

ACTUAL RESULTS OBTAINED IN F_2 FROM A CROSS INVOLVING THREE INDEPENDENT FACTORS COMPARED WITH THE THEORETICAL EXPECTATION

Phenotype Class	Ratio	Number of Seeds Ear 1		Number of Seeds Ear 2	
		Found	Expected	Found	Expected
Purple yellow starchy	27	54	54	64	57
Purple yellow sweet	9	20	18	10	19
Purple white starchy	9	18	18	23	19
White yellow starchy	9	16	18	18	19
White white starchy	3	6	6	12	6
White yellow sweet	3	6	6	4	6
Purple white sweet	3	6	6	4	6
White white sweet	1	3	2	1	2
	64	129	128	136	134

Recombination with a large number of differences.— When more units are involved the same principle of recombination holds, but the number of different combinations soon becomes so large that no one cares to work them all out. Table V shows the number of individuals that must be produced in order to secure all the different types when various numbers of character differences are used.

TABLE V

THE THEORETICAL NUMBER OF DIFFERENT CLASSES AND OF INDIVIDUALS NECESSARY TO OBTAIN THESE CLASSES IN THE SEGREGATING GENERATION FOLLOWING A CROSS INVOLVING DIFFERENT NUMBERS OF FACTORS

Number of Factor Pairs in Which Parents Differ	Number of Different Phenotypes	Number of Different Genotypes	Number of Individuals Necessary to Obtain All Different Types
1	2	3	4
2	4	9	16
3	8	27	64
4	16	81	256
5	32	243	1024
6	64	729	4096
n	2^n	3^n	4^n

Calculating ratios.—All the various ratios of recombination can be arrived at in a simple algebraic way. The basic formula is the binomial $a+b$. Multiplying this by itself, we get:

$$\begin{array}{r} a+b \\ a+b \\ \hline a^2+ab \\ \quad ab+b^2 \\ \hline 1a^2+2ab+1b^2 \end{array}$$

This is the monohybrid ratio of 1 : 2 : 1, or, when dominance is shown, 3 : 1. The exponents show whether the determiner is present once or twice. If this 3 : 1 ratio is multiplied by itself the dihybrid ratio is obtained, and this again multiplied by 3 : 1 gives the trihybrid ratio.

$$\begin{array}{r} 3:1 \\ 3:1 \\ \hline 9:3 \\ 3:1 \\ \text{or} \\ 9:3:3:1 \end{array} \qquad \begin{array}{r} 9:3:3:1 \\ 3:1 \\ \hline 27:9:9:3 \\ 9:3:3:1 \\ \text{or} \\ 27:9:9:9:3:3:3:1 \end{array}$$

These ratios may be combined in a large number of different ways. An illustration is found in oats, in which a black-hulled variety crossed with a brown-hulled sort gives 12 black, 3 brown, and 1 white. This is due to the fact that the 9 having both the black and brown determiners are black, just like the 3 which have black alone. Another common modification of the dihybrid ratio is obtained when one of the determiners can produce no visible effect except in the presence of the other. For example, the wild type of

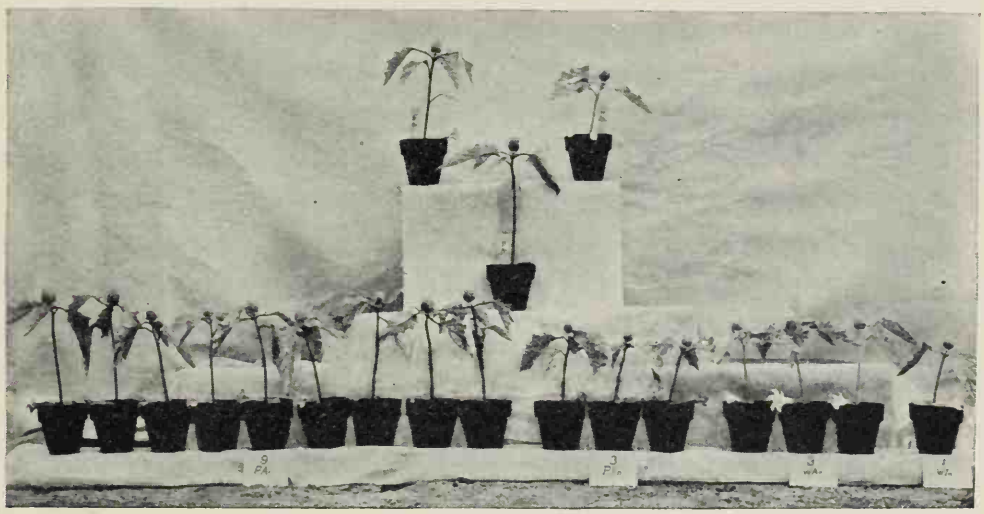


FIG. 38.—The 9 : 3 : 3 : 1 ratio illustrated by Datura. A plant with purple stems and flowers with spiny pods crossed with an uncolored plant with unarmed pods shows dominance of color and spines in F_1 with segregation in F_2 into the four possible combinations of pigmentation and spininess. (After Blakeslee in Jour. Heredity.)

guinea pig differs from some red varieties by two factors, one of which produces black pigment, while the other distributes this pigment in the characteristic manner which gives the wild agouti pattern. The result in the segregating generation from a cross of two such types is a ratio of 9 agouti, with both pigment and pattern determiners; 3 black, with the pigment but without the pattern; and 4 red. Three of the 4 red animals have the pattern, but this is unable to show without the black pigment. When neither of two determiners can produce an effect alone, the ratio

is 9 dominants to 7 recessives. In other cases, ratios of 13 : 3, 15 : 1, and 9 : 6 : 1 are met with, and these are to be considered as different groupings of the four parts of the basic 9 : 3 : 3 : 1 dihybrid ratio. Similar but more complex ratios are secured when a larger number of Mendelian differences is dealt with.

Characters dependent upon several determiners.—When purple and white varieties of corn are crossed, instead of segregating 3 : 1 into purple and white, they sometimes give purple, red, and white seeds. The red is a separate stage of color development, and true-breeding varieties with only red aleurone seeds have been produced. When such a red variety is crossed with some white varieties, instead of the red seeds which would be expected, purple seeds are formed. If it is assumed that two different determiners are necessary to produce the purple color, it is possible to account for these facts. One of these determiners, which may be called *R*, changes white seeds to red, and another, *P*, carries the reaction on to purple. Without *R*, the purple determiner is unable to operate and the seeds remain white. Such a variety, homozygous for the *P* factor, but without *R*, when crossed with red-seeded corn gives purple seeds in the F_1. In the next generation there are 9 seeds with both *R* and *P* and consequently purple, 3 with *R*, but without *P*, hence red; 3 with *P*, but without *R* and therefore colorless, and 1 lacking both *R* and *P* and also white. Therefore the ratio is 9 purple : 3 red : 4 white.

Multiple factors.—When more than one determiner takes part in producing a single visible effect, these controlling entities are usually called **multiple factors.** No essential distinction need be made between determiner and factor. Both terms are used more or less synonomously to designate the material transmitted by the gametes, which controls development. All the hereditary units are dependent upon other units for their proper expression. In most cases only a single difference exists. A character difference, when first found, may behave as a simple Mendelian dif-

ference. Later, other factors are found which also control this character or modify it in some way. This is well illustrated in corn. It has been found that many factors are necessary for both the *R* and *P* factors to produce color. One of these is called the *C* factor, and is considered to be a chromogen, a basic substance, which, when acted on by the enzyme *R*, is oxidized to a red color and makes it possible for *P*, if present, to carry the reaction on to purple. Recently, still another basic factor, *A*, has been found. *A*, *C*, and *R* must all be present before *P* can make purple. Without *P* the seeds are red, and if either *A*, *C*, or *R* are lacking, the seeds are white. A fifth factor, *I*, when present, prevents any color from appearing, no matter what other factors are there. It is called an inhibitor. It is, therefore, possible to have both dominant purple and dominant white.

This gives some conception of the great complexity of Mendelism. No one knows how many more factors are concerned with the production of color in the aleurone layer of corn. Such factors can be identified only when varieties are secured which lack them. As long as only one factor difference was known for aleurone color it was all right to give the formula of purple as *PP* and white *pp*. Now that five factors are known, the formula for purple is *AA*, *CC*, *RR*, *PP*, *ii*. Red aleurone corn is *AA*, *CC*, *RR*, *pp*, *ii*, and 30 different, pure-breeding, uncolored-aleurone varieties of corn are possible. Many of these when crossed among themselves will give color, as has been demonstrated. Multiple factors working together to produce certain effects have been demonstrated in many other plants and in animals. In the snapdragon, there are known to be 10 factors which regulate the color of the flowers and several others which control shape. Some 13 factors have been identified with the seed color of beans. The same situation is found in the coat color of rats, mice, and other mammals, in the color and patterns of birds, and also in insects.

Hybrids differing from either parent.—Bateson, in England, shortly after the rediscovery of Mendel's work,

crossed two white varieties of sweet peas and obtained purple flowers. When the second generation was grown, it segregated into approximately 9 purple to 7 white-flowered plants. He interpreted this to mean that there are two independent factors in the sweet pea, both of which must work together to manufacture color. That there are two separate factors is proved by the fact that some white-flowered plants when crossed together never give purple. It is only when the two complementary factors are brought into the same plant that color is formed.

Atavism.—It has long been noted that crossing tends to bring back ancestral characters. The original color of the wild sweet pea was purple. Two cultivated varieties which had given only white flowers were crossed, and the primitive purple flower was restored. For the first time the phenomenon of reversion to ancestral type was made intelligible. This has also been found to be true of other plants and animals. From the outline of the factor situation in corn, given above, it is easy to see how color can be produced by crossing two white-seeded plants. A white-seeded variety of corn with the formula *AA, CC, rr, pp,* pollinated by a plant of the composition *AA, cc, RR, pp,* also white, will give red seeds, or, crossed by *AA, cc, RR, PP,* will give purple. This has been done experimentally. It has long been recognized that crosses between different breeds of pigeons frequently bring back the wild type of plumage. In nearly all domesticated animals and plants, it is found that crossing often restores features previously possessed, but temporarily lost. This return to ancestral conditions was so generally known before Mendel's time that it was given the name of *atavism.* Mendelism gave the clue to the understanding of this phenomenon.

Duplicate factors.—Those cases in which several factors working together are necessary to produce a given effect are illustrations of **multiple factors.** A converse situation is known in which several independent factors can produce the same effect. These are called **duplicate factors.** One

of the first instances of this sort was furnished by Nilsson-Ehle from the color of the seed of wheat. In certain crosses of white and red varieties of wheat, colorless seeds appeared only about once in every 16 times. This was found to be due to two separate determiners, each of which alone can produce color. An important point is also found here in the fact that the depth of color in the red seeds varies in a series from dark red to almost colorless. This is considered to be due to the number of factors present. Each factor is supposed to add strength to the color. Two doses of each of the two factors gives more color than one dose, and with two factors five different stages are possible, viz., *aa, bb; Aa bb,* or *aa bB; AA bb* or *aa BB; AA Bb* or *Aa BB;* and *AA BB.* In F_2 most of the seeds are intermediate red, and the numbers diminish in the direction of either the dark or light colored seeds.

Intergrading characters.—This can be understood more clearly by examining the dihybrid ratio. If each member of a Mendelian pair is considered separately as one dose of a factor, and if there is no dominance, the 16 individuals making up the dihybrid segregating progeny vary in color, according to the number of dominant factors present, from 0 to 4. The number and composition of the individuals in each of the five classes are as follows:

Color of Seeds	Formula	Number of Single Factors	Number of Individuals in F_2
Dark red	*AA BB*	4	1
Red	*AA Bb* or *aA BB*	3	4
Medium red	*AA bb* or *aa BB*	2	6
Light red	*Aa bb* or *aa bB*	1	4
White	*aa bb*	0	1
			16

The largest numbers occur in the intermediate grades of color and the fewest in the classes of extreme dark or light

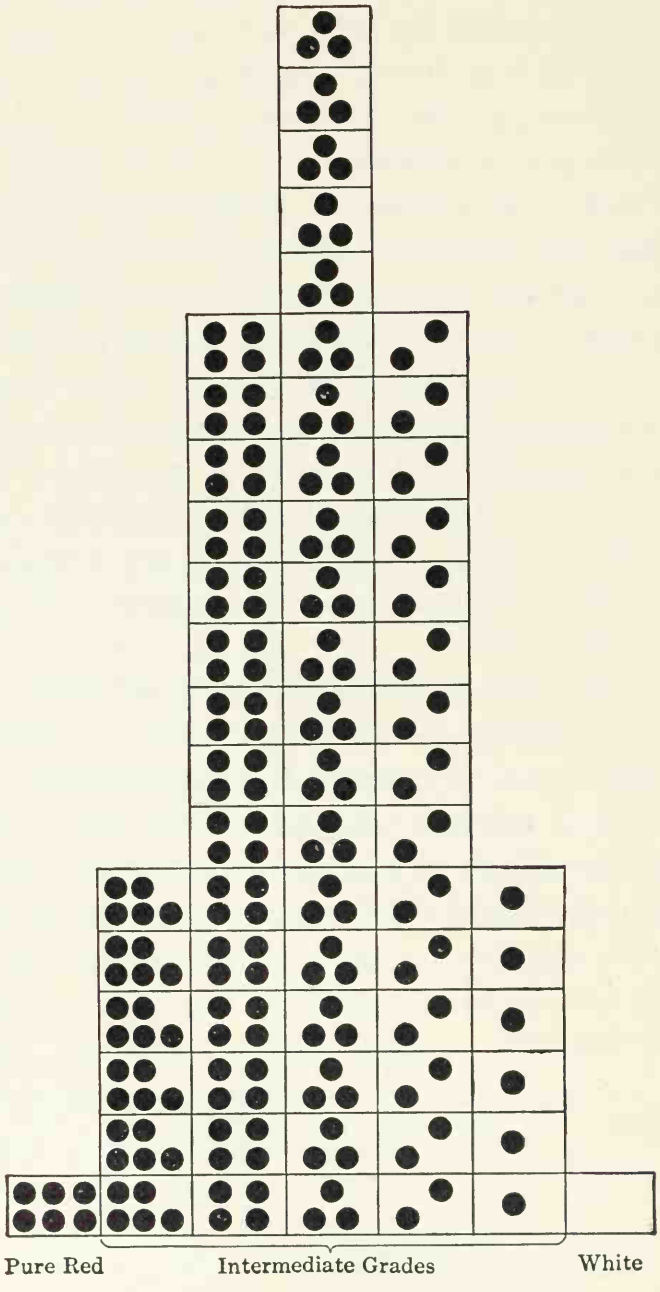


FIG. 39.—Diagram illustrating segregation in a continuously variable character, such as the red color in certain crosses of wheat. Six different intergrading classes are formed according to the number of single dominant factors they contain. The dots represent the number of color factors each individual has, and the squares represent the number of individuals in each class. (After Coulter and Coulter in "Plant Genetics," courtesy of the University of Chicago Press.)

color. There is gradation in color from one class to another so that it is not possible, upon inspection, to say definitely to which particular class any one seed belongs. Two seeds of apparently the same depth of color may have a different number of doses of the color factor, but there is a general range in color from light to dark.

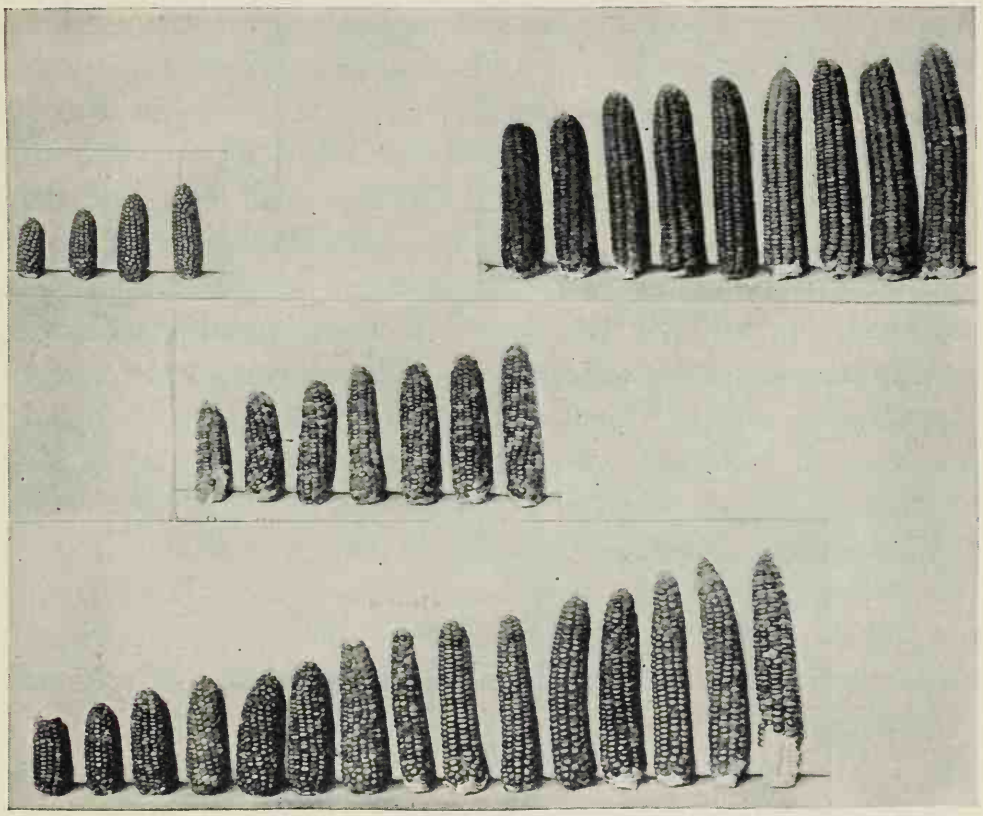


FIG. 40.—The result of crossing a short-eared pop corn with a long-eared sweet variety. The range in length of ear of the two parental varieties is shown above, with the F_1 and segregating F_2 generations below. (After East in American Naturalist.)

Other varieties of wheat found by Nilsson-Ehle differed by three factors. In the crosses of red and white, the F_1 seeds were intermediate in color and the second generation gave a large range in depth of color. Only about one individual in 64 was wholly lacking in color, and all taken together ranged gradually from light to dark, with most of the individuals in the intermediate grades. The theoretical

numbers expected in each grade are diagrammed in Fig. 39.

This is a basis for the understanding of many kinds of fluctuating or continuous variations. Most of the characters in which the plant and animal hybridizer is interested show such variation. Height of plant, size of fruit, weight of body, and nearly all general features of animals and plants vary in a continuous manner. Part of this variation is due to differences in the environment in which the organism develops. Much of the diversity, however, is due to the inheritance. For example, a small variety of pop corn, known as Tom Thumb, grows about 3 feet high and has ears from 2 to 5 inches in length. Both the height of plant and length of ear may vary according to the fertility of the soil and the rainfall; but never do these plants reach the height or size of ear of the larger, more commonly grown varieties of corn. When pop corn is crossed with larger varieties of field and sweet corn, the F_1 plants are intermediate in length of ear. The variation is not greater than that of either parent. When the second generation is grown there is a great range, as shown in Table VI. If sufficient numbers are grown, plants as small as one variety or as large as the other are obtained, but the bulk of the individuals

TABLE VI

THE DISTRIBUTION IN LENGTH OF EAR OF TWO VARIETIES OF CORN AND THEIR F_1 AND F_2 HYBRID PROGENIES

Data from East, *in American Naturalist*

Generation	Ear-length Classes in Cm.																	Number of Plants Grown
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
P	4	21	24	8	..	..	..	..	..	..	..	..	..	..	..	..	..	57
P	..	..	..	..	..	..	..	..	3	11	12	15	26	15	10	7	2	101
F_1	..	..	..	..	1	12	12	14	17	9	4	..	..	..	..	..	..	69
F_2	..	..	2	5	17	33	33	33	27	21	13	10	11	12	1	2	1	221

are in the intermediate grades. If the variation within either of the parental varieties is due to external influences, the difference in the extent of variability between the first and the second generation hybrids must be due to recombination of hereditary factors.

In this illustration there are a large number of factors involved in the differences between the two varieties. After crossing, segregation and recombination take place, so that new combinations are made, as well as the parental types. As most of the individuals obtained in F_2 are heterozygous for a large number of factors, they will not breed true for their particular size, but their progeny will tend to resemble them. By growing the progeny so as to prevent crossing, and selecting for several generations, it is possible to fix a new size.

Inheritance of size and other quantitative characters.— In this way the Mendelian inheritance of size and other indefinite quantitative characters has come to be understood. For the most part, there are many factors involved and it is seldom possible to pick these out individually. Take, for example, height of plant. Every factor which influences growth may indirectly affect height. The internode length, number of internodes, the root development, amount, and quality of the chlorophyll and the fibers in the stem are all concerned with height in some way. All these may differ in the effect they have. Some probably influence size much more than others. The matter is further complicated by interdependence of characters. A large ear of corn can be produced by a large plant, but such an ear could not be borne on a small plant even if the particular ear factors for large size were present.

The inheritance is to be considered as made up of a number of comparatively definite, stable units. A plant or animal should not, however, be thought of as a mosaic of different characters. Each individual is the result of growth in which all the inherited potentialities work together. It is their harmonious interaction under the influence of the

external environment that brings each individual to be what it is.

Some of the reasons why it is possible to consider the inheritance of size and growth characters as Mendelian and as essentially the same in principle as the transmission of the more clear-cut qualitative differences are as follows:

1. Crosses between pure races give first generation progenies as uniform as the parental types.

FIG. 41.—Range in height of plant of a small variety of pop corn and a large variety of dent corn. (After Emerson and East in Nebraska A. E. S. Research Bull. 2.)

2. Variation is greater in the second generation than in the first.

3. When a sufficient number of individuals are obtained the grandparental types are recovered.

4. Variations which exceed the extremes of either parental race are sometimes obtained, because new combinations are brought about and some of these may cause a greater or less development of certain characters than that produced by either parent.

5. Different lines descended from second generation individuals differ in their variability and in the length of time necessary to reduce them to uniformity and constancy, because some combinations are composed of like elements in all of their paired factors and therefore remain constant, while others are made up of unlike elements and again segregate.

Application of Mendel's principles.—With these main

FIG. 42.—Range in height of plant of the segregating F_2 generation from the cross of the tall with the short variety shown in Fig. 41. (After Emerson and East in Nebraska A. E. S. Research Bull. 2.)

features established, Mendelism has been found to be applicable to all the important characters of animals and plants. In animals, the weight of body, length of ear, shape of skull, time required to reach sexual maturity, number of feathers, egg-laying capacity, etc., have been shown to fulfil these general requirements. In plants, the number of leaves of tobacco, rows of grain on the ear of corn, time of flowering in peas, and resistance of corn to the smut

fungus are a few of the many examples which show segregation and recombination. Many complications have arisen, and in a number of instances the details of inheritance are not clearly understood. But in all these cases where Mendelian inheritance does not seem to fit the facts, no other method of inheritance has been proposed which fits them better. Mendelism has therefore the greatest value to the plant and animal breeder. By its aid variability is understood to be due partly to the environment, partly to heredity. It is with the inherited variations that the breeder is chiefly concerned. The machinery for the transmission of characters furnishes a means by which heritable variations can be induced by crossing and fortunate combinations of characters can be selected and fixed. It is, therefore, necessary to understand the mechanism of heredity as clearly and as fully as possible. For this purpose our attention will now be directed to the carriers of the inheritance.

CHAPTER V

THE CARRIERS OF THE INHERITANCE

One of the early conceptions resulting from Mendel's work was that all the units of inheritance were distributed independently of each other at the formation of the reproductive cells. Very soon after interest in the testing of the new principles of heredity was awakened, it was found that character arrangements contributed by each parent to the hybrid sometimes tend to stay together in the formation of the hybrid's progeny. Although recombination of all characters is brought about, the numbers obtained are not always those expected to result from pure chance assortment. One of the first instances of this was observed by Hedrick and Booth at the Geneva Experiment Station while they were applying the principles of segregation and recombination to characters in the garden tomato. Their results were reported in 1907. A cross of a variety with pear-shaped fruit and tall vine with a dwarf variety with round fruit showed dominance of the standard vine and non-constricted fruit. In the second generation, instead of obtaining the four assortments of these two characters in the usual ratio of 9 : 3 : 3 : 1, the investigators found a large excess of the parental types and very few of the new combinations. A total of 452 plants were grown, and among these the double recessive, having dwarf plant and constricted fruit, appeared only three times. With independent segregation, more than nine times this number were looked for. A similar coherence of characters in transmission has been observed in other plants and in animals. The first case to be carefully studied was that of sweet peas, observed by Bateson at the John Innes Horticultural Institute in England. Some

varieties of this flower are distinguished by long pollen grains instead of round. From a cross of a purple-flowered plant with long pollen and a red variety with round pollen, the same tendency toward the persistence of the parental grouping of characters was noted.

Factors transmitted together.—With independent segregation, gametes carrying the different factors are formed in equal numbers. This is shown by back-crossing a hybrid with the recessive parent. In this particular case the hybrid plant with purple flowers and long pollen grains back-crossed with a round-pollen, red-flowered plant, should

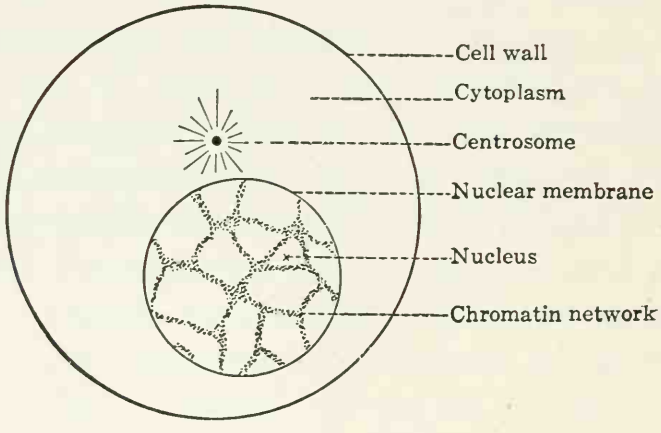


FIG. 43.—Diagrammatic representation of a single cell. (After Walter in "Genetics," courtesy of Macmillan Co.)

give, with independent inheritance, the following four types in equal numbers: purple long, purple round, red long and red round. Actually there were grown 50 purple long, 7 purple round, 8 red long and 47 red round plants. The parental groupings of characters were restored in large numbers. The new arrangements were very few. The count was roughly in the proportion of 7 : 1 : 1 : 7, indicating that the four different kinds of gametes were formed in this ratio instead of an equal number of each. When the new combinations—in this instance, purple-flower round-pollen, and red-flower long-pollen were crossed—the same phenomenon was observed. Both the new combinations, as they went into the cross from the parents, now

tended to stay together and separated only a small number of times. The red-long and purple-round plants were much in excess, while the reverse classes were few in number, just the opposite to the result obtained before.

Before these facts could be explained, the machinery by

FIG. 44.—Photograph of dividing cells in the grasshopper. The black rod-shaped bodies are the chromosomes which are being pulled apart by the threads on the spindle. In ordinary cell division, each chromosome splits, the halves move to opposite poles, and a new cell wall is laid down between the two groups. Each of the two daughter cells thus contains the same number of chromosomes as the original cell. On account of their being greatly enlarged, only a few of the chromosomes are in focus in the picture. (After Carrothers.)

which the hereditary determiners are rearranged and transmitted from one generation to the next had to be understood. Credit for making clear the actual process of transmission is due in large part to the cytologists, whose investigations have extended over many years. Many facts have been accumulated, and important discoveries

are still being made. It is possible here to give only the most essential features of this process.

The structure of living organisms.—Every animal or plant, no matter what its form, is made of units of structure called **cells.** These differ greatly in size, shape, and other characteristics, according to the kind of tissues they are in, but they all have certain features in common. When in an active growing condition, their outer part is made up of a more or less clear, jelly-like substance, the **cytoplasm,** which surrounds a spherical mass known as the **nucleus.**

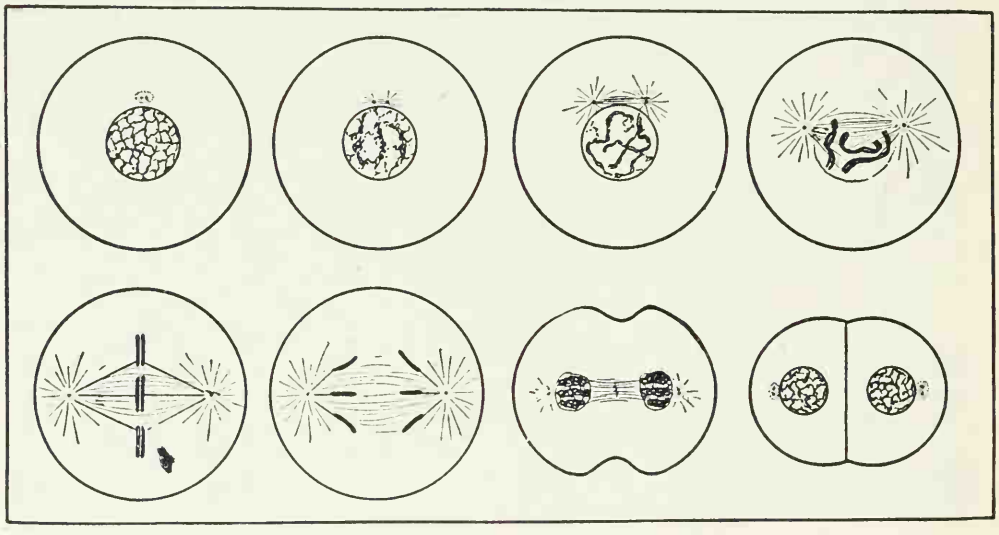


FIG. 45.—Diagrammatic representation of the behavior of the chromosomes during cell division in growing tissues. (After Sharp in "Introduction to Cytology," courtesy of McGraw-Hill Book Co.)

Both the nucleus and cytoplasm are usually enclosed in membranes. When cells are viewed under the microscope the nuclei are seen to be largely composed of a granular substance, which has the property of being deeply stained by certain dyes. These dyes are used for the purpose of making the details of structure more easily apparent. At certain stages, particularly when the cell is getting ready to divide, the granular substance assumes the appearance of definite bodies, spherical or rod-shaped in form. There may be a few or many of these structures in each cell of one animal or plant, but their number is generally constant

for every species. When the cell divides, each of these bodies, called **chromosomes** because they stain more deeply than other parts of the cell, also divides equally, one set going to one daughter cell and one to the other. In this way the cell reproduces itself in the process of growth and development of the organism.

Formation of the germ cells—Early in the life history of the plant or animal, certain cells are set apart for sexual

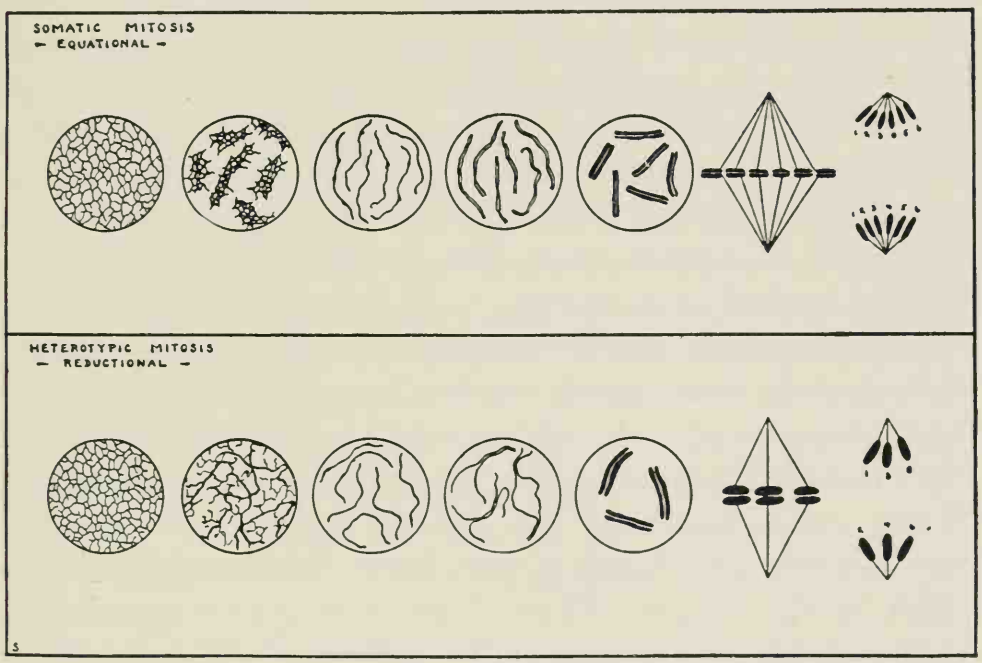


FIG. 46.—Diagrammatic representation (below) of the behavior of the chromosomes during the formation of the germ cells compared with their behavior in somatic division (above). (After Sharp in "Introduction to Cytology," courtesy of McGraw-Hill Book Co.)

reproduction. When the time comes for the formation of the male and female germ cells, the chromosomes of each of these cells come together in pairs and partially fuse. When the cells divide, the two members of each pair of chromosomes separate, one set going to each of the two daughter cells. There is not a division of the individual chromosomes, as in ordinary cell multiplication in growth, but only a separation of the chromosomes which have previously paired. In this way the number of chromosomes is

always reduced one half, in preparing the germ cells for sexual reproduction. For example, in the sweet pea, the plant cells have 14 chromosomes while the egg cells and pollen grains each have 7. When the egg and sperm unite, the original number of chromosomes is restored, and this number continues throughout the development of the plant until the time comes again for reproduction.

Parthenogenesis.—In those comparatively rare cases where seed is formed when pollen is excluded, it has been found that there is usually no reduction in the number of chromosomes. In some cases the embryo is not formed from the egg cell but from some vegetative cell in the ovary. Such cases of **parthenogenesis,** or **vegetative apogamy,** are essentially merely a form of vegetative reproduction. In this form of reproduction, the hereditary composition is usually handed on unaltered.

Mechanism of sexual reproduction.—In the chromosome system there is an orderly mechanism adapted both for the multiplication of cells, which takes place in growth, and for the multiplication of individuals by sexual reproduction. Every cell of the body has a set of paired chromosomes; one member of each pair is contributed by the male and the other by the female. These chromosomes vary in size and shape at different stages in the growth of the cell and in different cells; but in many cases the chromosomes differ among themselves, and by their characteristic differences they can be traced from cell to cell and from individual to individual. It is well established that the chromosomes retain their individuality. The evidence is convincing that the inheritance of every individual consists mainly of substances which are carried in the chromosomes and which are capable of directing the development of each individual along definite lines. Naturally, the resulting size and form of the adult depend a great deal upon the surroundings in which it develops, but many of the minor as well as major details which set off each individual from every other individual are due to hereditary **determiners** carried in the

chromosomes. To make the operation of this machinery clear, it is necessary to follow single characters from one generation to another.

Hereditary determiners located in the chromosomes.— In the case of the tall and dwarf tomato previously described, it is assumed that the determiner for short growth is located at a definite place in one of the chromosome pairs. There are two of these determiners, exactly alike and placed in the same relative position, one in each member of one pair of chromosomes. At the formation of the reproductive cells, the two chromosomes, both carrying the determiner for dwarfness, come together in preparation for cell division. At the reduction division they separate, one chromosome going to one daughter cell, the other chromosome to the other cell. In the reproductive cells, therefore, there is only one member of this particular chromosome pair carrying the determiner for dwarfness. If the dwarf plants are self-pollinated or pollinated by another dwarf, the egg containing the chromosome with the one dwarf determiner meets the sperm containing the same chromosome with with the other dwarf determiner. The doubled condition of the chromosomes is restored and the resulting plant is dwarf.

In the tall tomato, the same place on the corresponding chromosome pair is occupied by a different determiner, which in some way causes the plant to grow tall. The reduction division takes place as in the dwarf plant; and when cross-fertilization between these two types occurs, the set of chromosomes from the tall plant meets the set from the dwarf plant, so that in the pair of chromosomes carrying the height determiners the two members are unlike with respect to this one determiner.

Although the germ cells fuse together in the process of fertilization, there is no blending of the chromosomes or the determiners they carry. *Each chromosome retains its individuality, and the determiners themselves are unmodified by contact with different determiners.* At the reduction division

the homologous chromosomes (members of the same pair) containing the different determiners separate, the one for tall growth going to one daughter cell, the one for short growth to the other. In this way each gamete carries only one of the two possible determiners for height, and never both. When the hybrid is self-pollinated or pollinated with a similar hybrid plant, the gametes have an equal chance to unite with like or unlike gametes and give the 1 : 2 : 1 Mendelian ratio already described.

Different factors carried by the same chromosome.—The association of characters from one generation to the next, such as Bateson found in the sweet pea between pollen shape and flower color, is easily explained if it is assumed that the different determiners are located on the same chromosome. Convincing evidence has been furnished by Morgan and his students, Bridges, Sturtevant and Muller, who have been chiefly responsible for the development of the chromosome theory of heredity, that many factors are located in the same chromosome pair. These factors are held together in groups, and segregation is not independent between factors in any one group. It is only the different chromosomes which recombine freely. Any given factor in one chromosome pair is independent in transmission from all other factors carried in any other chromosome pair, but not with the others joined with it.

Breaks in the linkage.—The chromosomes as carriers of the inheritance explain very nicely why certain characters are coupled in transmission; but according to this theory they should always be coupled. The reversed associations which have been obtained must be accounted for. To do this it is necessary to suppose that a piece of one member of a chromosome pair may break loose and be exchanged with the corresponding piece of the other member. It is assumed that the character-determining factors, or **genes** as they are now called, are distributed along the chromosome at definite points, or **loci,** and the distance between any two loci determines the frequency with which they separate

from each other. Factors carried by one chromosome are said to be **linked** and, when separation occurs, it is due to breaks in the **linkage.** The disunions are considered to occur at some stage before the germ cells go through the reduction division. At that time the chromosomes are observed to come together and pair, and sometimes they twist about each other. When they are separated at the division of the cells, they may break, and part of one chromosome may go with the remaining piece of the other chromosome, as shown diagrammatically in Fig. 47. The breaks can occur at any point in the strand, so that the frequency with which interchange or **crossing-over** takes place between any two points depends on their distance apart. The further apart the genes are located, the more often will they be disjoined, while two points close together will be rarely separated.

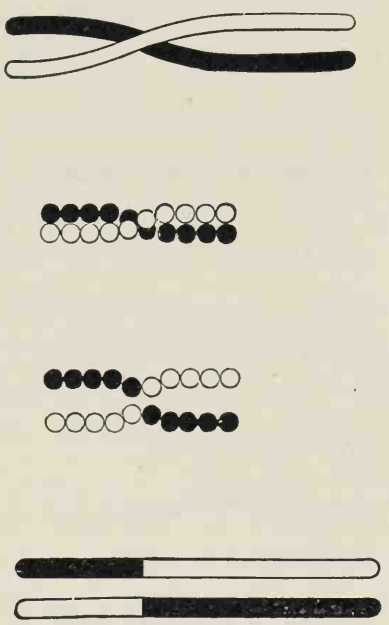


FIG. 47.—Diagram illustrating crossing-over of chromosomes. (After Morgan in "A Critique of the Theory of Evolution," courtesy of Princeton University Press.)

Explanation of linkage.—According to this conception, the factors for pollen shape and flower color in the sweet pea are carried in the same chromosome. In the first cross mentioned, the genes for purple flower color and long pollen shape, contributed by one parent, are in one member of a chromosome pair, and those for red flower and round pollen, contributed by the other parent, are in corresponding loci in the other member of the pair. During gamete formation, in one out of every eight cells the chromosomes break somewhere between these two points and an interchange occurs. In the other cells no crossing-over takes place. It makes no difference whether two dominant factors are in one chromosome and two recessives in the homologous member,

or one dominant and one recessive are in each. Interchange is made the same number of times, so that the parental combinations, whatever they may happen to be, tend to stay together and in the same degree.

Groups of factors.—When the sweet pea was further investigated, other factors were found to be in this chromosome. Position of the petals is associated with flower color and pollen shape. Evidently this third gene lies closer to the one for purple, as the breaks in the linkage are much less frequent than between flower color and pollen shape. When purple flower with erect petals is crossed with red and hooded flower, the new combinations in the gametes, as shown by back crosses, are formed only about once in every 128 times. Other groups of factors have been found in the sweet pea, such that recombinations within any one group is restricted whereas between any two factors in different groups rearrangement is perfectly free.

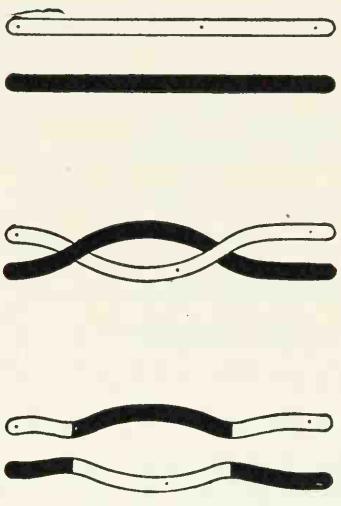


FIG. 48.—Diagram illustrating double crossing-over. (After Morgan in "A Critique of the Theory of Evolution," courtesy of Princeton University Press.)

Chromosomes as carriers of the inheritance.—A large number of circumstances point conclusively to the chromosomes as the main carriers of the inheritance. Whenever there is abnormal distribution of the chromosomes resulting from imperfect cell division, pronounced changes in the individual usually result. In certain cases, pieces of chromosomes and even whole chromosomes have been lost, and the individuals with such deficiencies are sometimes lacking in certain characters. Such irregularities have a visible effect only in heterozygous individuals when the dominant factors are lost. Moreover, there is indirect evidence to show that the chromosomes are the carriers, in

the fact that the inheritance is derived in approximately equal amounts from the male and from the female, although there is an enormous difference in the size of the two kinds of reproductive cells. The amount of **chromatin,** the substance of which the chromosomes are made, is nearly the same in the egg and in the sperm. The chromosomes make up the main contents of the nuclei. As far as has been observed, only the nucleus of the sperm enters the egg and takes part in the fusion. There is the possibility that a small amount of cytoplasm may enter in some organisms, but this has not been clearly demonstrated. In some experiments with lower animals, the nucleus has been taken out of the egg; when such an enucleated egg was fertilized by a sperm cell from a different species, the characters of the resulting individuals were entirely paternal. Finally, the reduction division, which halves the number of chromosomes, takes place only in preparation for sexual reproduction and is an orderly process which serves the exact purpose needed to account for the known distribution of inherited factors.

Transmission through the cytoplasm.—In plants, small bodies called **plastids** are situated in the cytoplasm and are transmitted from one generation to another in the cytoplasm of the egg. These plastids contain the chlorophyll. They multiply in numbers by division, in somewhat the same way that the cell divides, and are handed on directly from one cell to another. In certain abnormal forms, these plastids have lost the power to produce the green coloring matter which they normally contain. Tissues containing these defective cells are white. Whole branches may be formed from these colorless cells, and such branches are in strong contrast to the normal green condition. Sometimes flowers which produce pollen and seeds are formed on these white branches. These seeds produce only colorless plants, which die whether fertilized with their own pollen or with pollen from normal green branches. Normal flowers, fertilized by pollen from the white branches, produce normal

green seedlings and never show the deficiency in later generations. This type of inheritance is purely maternal. The deficiency is never transmitted through the pollen; and when normal plastids are lacking in the egg, they can not be restored by normal pollen. This type of inheritance is comparatively rare and is in marked contrast with numerous cases of total lack of chlorophyll, which gives a similar result but is controlled by factors carried in the chromosomes in both the egg and pollen. Although there is still the possibility that some other unrecognized parts may have something to do with transmission, all of the facts so far known confirm the general applicability of the chromosome theory of heredity, and this mechanism makes clear many perplexing problems in the transmission of the inheritance.

Experiments with Drosophila.—By far the most complete evidence has been supplied by an insect, the tiny fruit fly (*Drosophila melanogaster*), which is common about the house whenever fruit is spoiling. This lowly creature has made possible some of the most remarkable and valuable biological experiments in modern times. Drosophila is particularly favorable as material for researches in heredity, because a large number of offspring are secured from each mating, the life cycle is short, and many character differences are known. Moreover, this organism has only four pairs of chromosomes. According to the chromosome theory of heredity, no matter how many character differences are discovered in this insect, they must all be in four groups. These groups will show independent segregation with each other, but within each group there must be linkage. About 150 factors are so far known in Drosophila, and

FIG. 49.—Diagram representing the comparative size and shape of the four pairs of chromosomes in *Drosophila melanogaster*. (After Morgan in "A Critique of the Theory of Evolution," courtesy of Princeton University Press.)

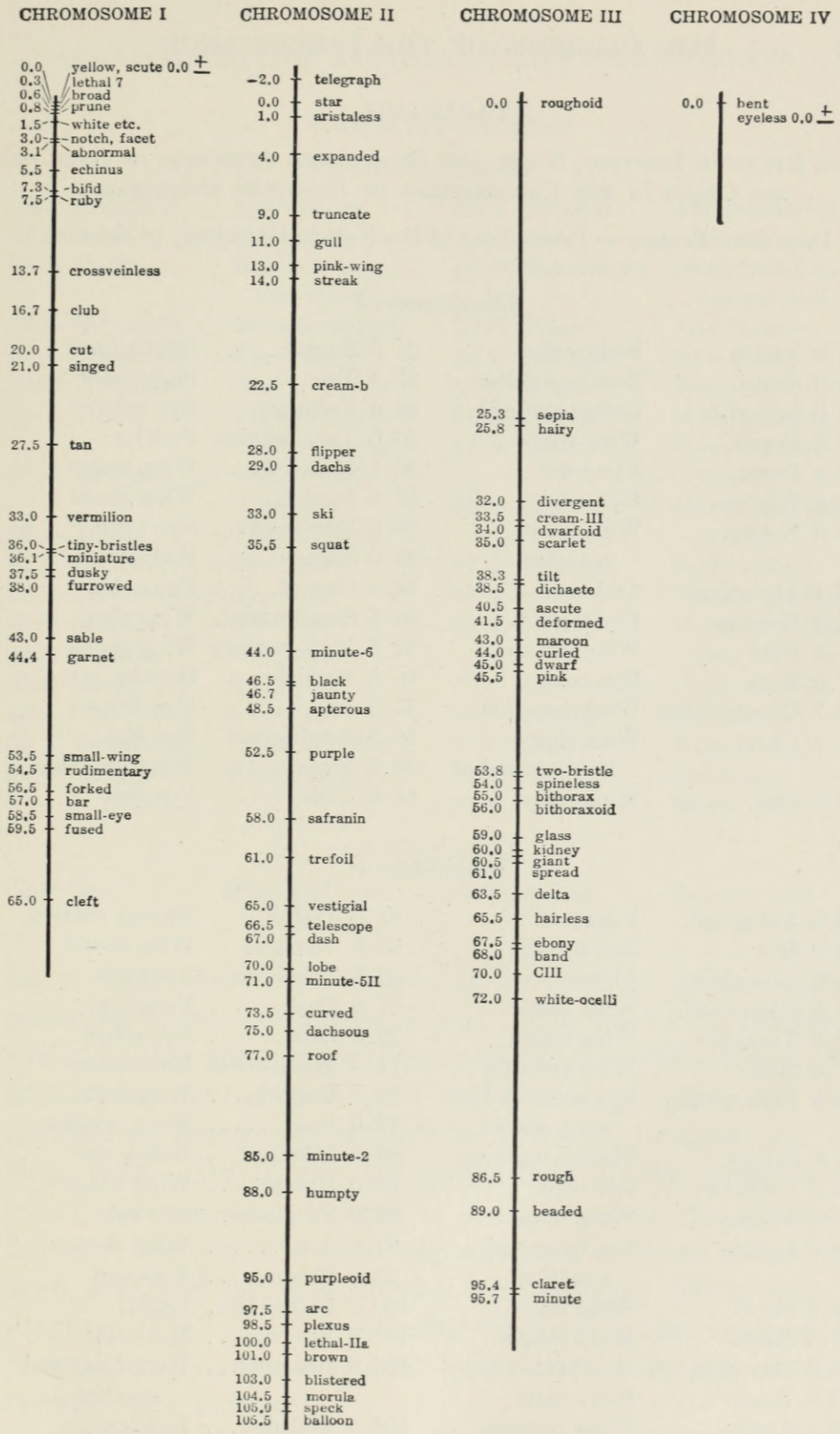


FIG. 50.—Map of the four chromosomes of *D. melanogaster* locating some of the factors that have been most fully studied. The distances between the loci represent the average amount of crossing-over between those points. (After Sharp in "Introduction to Cytology," courtesy of McGraw–Hill Book Co.)

TABLE VII

THE RELATIVE POSITION, NAME, AND CHARACTERS AFFECTED, OF SOME OF THE GENES IN THE CHROMOSOMES OF *Drosophila Melanogaster*

Data from Bridges in Proceedings of the National Academy of Sciences

Chromosome I

0.0	Yellow	Body color	21.0	Singed	Bristle form
0.0	Scute	Bristle number	27.5	Tan	Body color
0.3	Lethal 7	Lethal (tumor)	33.0	Vermilion	Eye color
0.6	Broad	Wing shape	36.0	Tiny bristles.	Bristles
0.8	Prune	Eye color	36.1	Miniature	Wing shape
1.5	White	Eye color	37.5	Dusky	Wing shape
3.0	Notch	Wing shape, venation	38.0	Furrowed	Eye form
			43.0	Sable	Body color
3.1	Abnormal	Abdomen	44.4	Garnet	Eye color
5.5	Echinus	Eye texture	53.5	Small wing	Wing size
7.3	Bifid	Wing venation	54.5	Rudimentary	Wing shape
7.5	Ruby	Eye color	56.5	Forked	Bristles
13.7	Crossveinless	Wing venation	57.0	Bar	Eye shape
16.7	Club	Wing shape, bristle number	58.5	Small eye	Eye size
			59.5	Fused	Wing venation
20.0	Cut	Wing shape	65.0	Cleft	Venation

Chromosome II

−2.0	Telegraph	Venation	61.0	Trefoil	Thorax pattern
0.0	Star	Eye texture	65.0	Vestigial	Wing shape
1.0	Aristaless	Arista	66.5	Telescope	Abdomen
4.0	Expanded	Wing shape	67.0	Dash	Venation
9.0	Truncate	Wing shape	70.0	Lobe	Eye shape
11.0	Gull	Wing position	71.0	Minute-5-II	Bristle size
13.0	Pink wing	Eye color and wing shape	73.5	Curved	Wing form
			77.0	Roof	Wing position
14.0	Streak	Thorax marking	85.0	Minute-2	Bristle size
22.5	Cream-*b*	Eye color	88.0	Humpy	Wing shape
28.0	Flipper	Wing shape	95.0	Purpleoid	Eye color
29.0	Dachs	Leg form and venation	97.5	Arc	Wing shape
			98.5	Plexus	Venation
33.0	Ski II	Wing shape	100.0	Lethal II*a*	Lethal
35.5	Squat	Body shape	101.0	Brown	Eye color
44.0	Minute-6	Bristle size	103.0	Blistered	Wing form and venation
46.5	Black	Body color			
46.7	Jaunty	Wing position	104.5	Morula	Eye texture
48.5	Apterous	Wingless	105.0	Speck	Wing spot
52.5	Purple	Eye color	105.5	Balloon	Wing form
58.0	Safranin	Eye color			

TABLE VII—*Continued*

Chromosome III

0.0	Roughoid	Eye texture	55.0	Bithorax	Differentiation in thorax
25.3	Sepia	Eye color			
25.8	Hairy	Hairs on wing and thorax	56.0	Bithoraxoid	Duplication in metathorax
32.0	Divergent	Bristle position	59.0	Glass	Eye texture
33.5	Cream III	Eye color	60.0	Kidney	Eye shape
34.0	Dwarfoid	Size	60.5	Giant	Body size
38.3	Tilt	Venation and wing position	61.0	Spread	Wing position
			63.5	Delta	Venation, eye texture
38.5	Dichaete	Bristles and wings	65.5	Hairless	Bristle and hair number
40.5	Ascute	Thorax shape			
41.0	Scarlet	Eye color	67.5	Ebony	Body color
41.5	Deformed	Eye form	68.0	Band	Thorax marking
43.0	Maroon	Eye color	70.0	C III	Cross-over variation
44.0	Curled	Wing shape			
45.0	Dwarf	Body size	72.0	White ocelli	Color of ocelli
45.5	Pink	Eye color	86.5	Rough	Eye texture
53.8	Two-bristle	Bristle number	89.0	Beaded	Wing form
54.0	Spineless	Bristle size	95.4	Claret	Eye color
			95.7	Minute	Bristle size

Chromosome IV

0.0	Bent	Wing and tarsal form	0.9	Eyeless	Eye size and shape

all of these have been found to be in four groups corresponding to the four chromosomes. The size of the chromosomes in this organism differs considerably, there being one small pair, one medium pair, and two large pairs, and the number of hereditary differences is fairly proportional to their bulk. By taking the percentage of the gametes in which crossing-over occurs as a measure of the distance between the genes in each chromosome, a linear series has been arranged for each of the four groups. With such a diagram (Fig. 50) it is possible to predict the amount of crossing-over, and hence the possibility of recombination, between any two loci.

Arrangement of factors in the chromosomes.—A feature of the situation so far portrayed in Drosophila is that the characters do not seem to be arranged in any definite way.

The factors which control color, for example, are not all in one chromosome or even in a part of one chromosome, nor are the genes which have to do with wing shape in

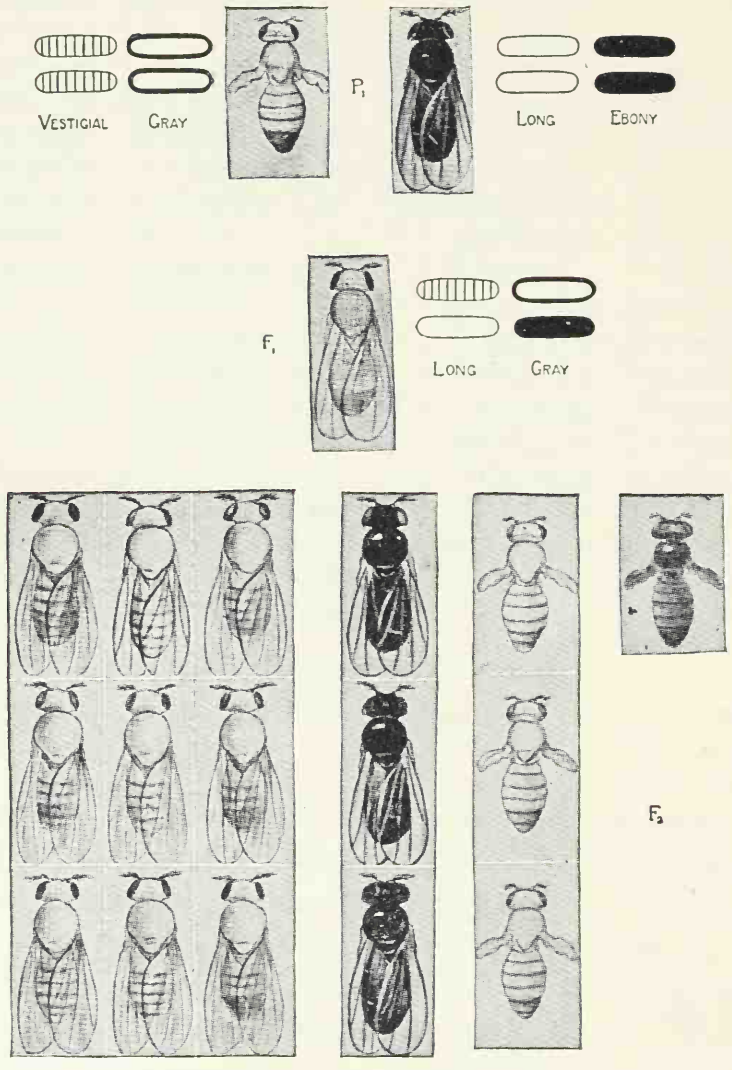


FIG. 51.—Cross between a long-winged, ebony-bodied fly and a vestigial-winged, gray-bodied fly, showing recombination of factors located in different chromosomes. (After Morgan in "A Critique of the Theory of Evolution," courtesy of Princeton University Press.)

another, nor those of body size in a third; but all the characters of the fly seem to be distributed throughout all the chromosomes. Some of the Mendelian determiners in the four groups of Drosophila, classified according to the

part of the body they principally affect, and in the order in which they are arranged, are shown in Table VII.

Single factors having manifold effects.—Each factor represents a definite place on the chromosome which in some unknown way affects the various parts of the body. Very often a factor may have an influence on widely different parts of the body. For example, one is known to govern

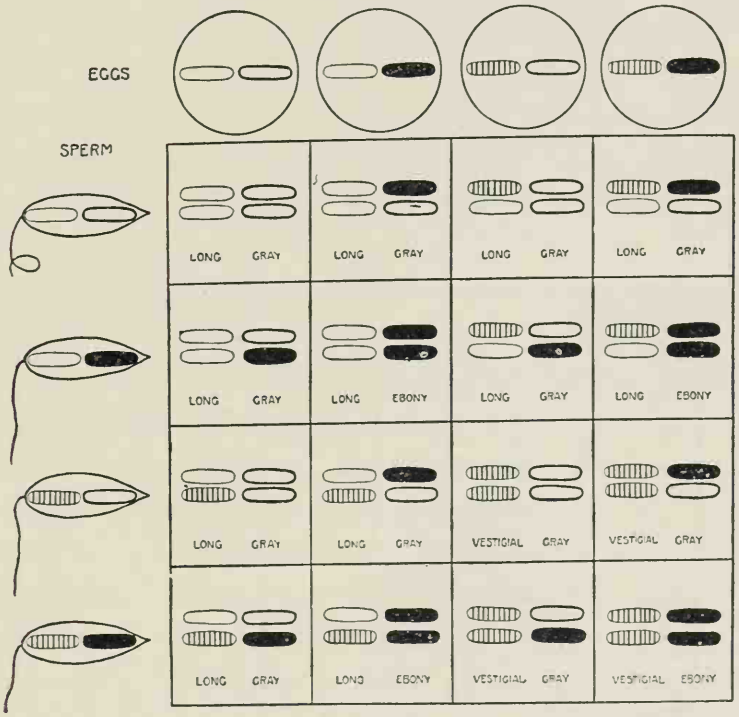


FIG. 52.—Diagram to show the history of the factors in the cross shown in Fig. 51. (After Morgan in "A Critique of the Theory of Evolution," courtesy of Princeton University Press.)

both the number of bristles on the thorax and the position of the wings. Note also that many different factors affect the same part of the body. All of the members within a group are linked in various degrees with every other gene in the same chromosome but show independent inheritance with any representative of another group.

Multiple allelomorphs.—Multiple factors affecting the same character are situated at different places in the chromosome mechanism. In contrast to this state of

affairs, a single factor may have many different forms, each of which produces a different result. For example, the red eye in Drosophila is controlled by a single factor. There was found to be a variation in this factor which makes the eyes white. Still later, another variation appeared, giving

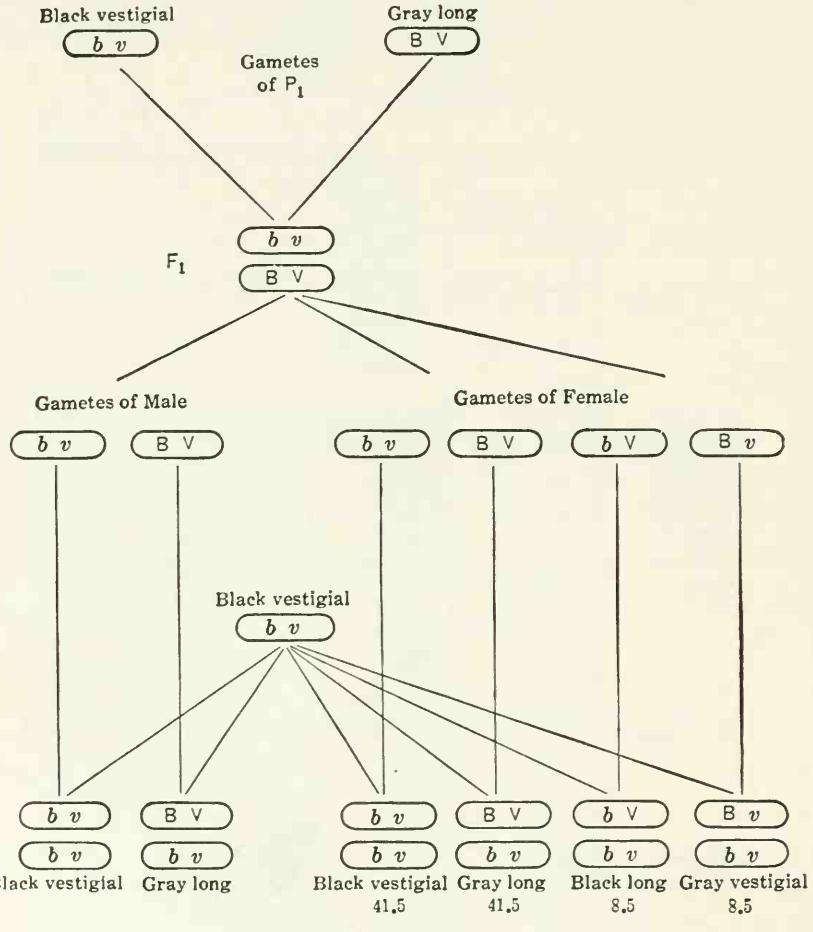


FIG. 53.—Cross between long-winged, gray-bodied and vestigial-winged, black-bodied fly, showing crossing-over between factors located in the same chromosome. (After Morgan in "A Critique of the Theory of Evolution," courtesy of Princeton University Press.)

cherry eyes. Many other differences in shade of color belonging to the same series have since been discovered. All these are due to changes in a single factor. Factors located at the same point on the chromosome, but in different members of the chromosome pair, are called **allelomorphs,** and such a set of factors as for eye color is known as a

series of **multiple allelomorphs.** No more than two allelomorphs can be present in one individual ordinarily. When individuals with different allelomorphs are crossed, only those that went into the cross are gotten out. For example, red-eyed insects crossed with white-eyed forms give all red eyes in the first generation because red is dominant over white, and in the second generation red- and white-eyed individuals are obtained. Similarly, white with cherry gives white and cherry eyes, but never red, and red and cherry never give white. A similar series exists in the pericarp color of corn. There are varieties with red ears, white ears, and striped ears. Crossing any two of these gives in the second generation only the two types that went into the cross

Linkage in other forms of life.—No other organism has furnished the wealth of data that this valuable insect has afforded, but sufficient evidence is fast being gathered to show that the chromosome mechanism is much the same for all animals and plants. In sweet peas, five groups with two or three factors in each are already known, as is one group of five in the primrose. The garden pea gives evidence of four linked groups. Corn has ten or twelve chromosomes, and up to the present time eight linked groups have been discovered, all independent of each other. No instances have been found in any organism where the number of independent groups exceeds the number of chromosomes.

Lethal factors.—In Drosophila, many of the new-found characters are relatively of minor importance in the life processes of the organism. Color of eye and body, position of the wings, number of bristles, and markings over the entire body, for the most part, are not greatly concerned with the vital functions. Other characters are very important, and some are absolutely essential for life. It has been found that there are a number of factors, the absence of which causes the death of the flies. These are the so-called **lethal** factors, and they are distributed throughout the chromosomes. All such factors must be recessive; other-

wise they would cause the death of the individuals in which they originate. The heterozygotes are able to live, but the recessive segregate dies. When lethal factors are involved, the progenies are smaller than normal. Very often, with lethal factors, perfect dominance is not shown, so that the hybrids can be distinguished from the pure normal type. When such is the case, a ratio of 1 normal to 2 heterozygotes is obtained, the one recessive being eliminated. One of the first instances of this kind was found in mice. A form of yellow mouse, when mated with others of the same color, gives offspring in the ratio of 1 normal gray to 2 yellow. Yellow mice always produce some gray animals and can not be obtained pure for the yellow color. As the litters are, on the average, smaller than litters from other mice, it is evident that the factor which produces yellow color in the heterozygous state represents a deficiency in some important function, and that therefore animals lacking both normal genes are unable to live. Recently, about one-fourth of the embryo mice have been found dead in the uterus of the mother in matings of yellow and yellow.

Hybrids that breed true.—In corn there are several factors which stop the development of the seed immediately after fertilization. Other factors in many plants and animals spell the death of the individual possessing them in double dose, without the normal factors to offset their injurious effects. Such lethal factors upset ordinary Mendelian expectations. Certain classes are prevented from appearing, and the proportions of heterozygous or inconstant individuals in a population is increased. Because lethal factors are recessive, they can remain indefinitely in stocks that are widely crossed. When two different lethal factors are present together in one individual, most unusual results are obtained, as shown by Muller in recent work with Drosophila. In his experiments it was found that two lethal factors lying in separate loci were in different members of the same chromosome pair. The composition in respect to other factors associated with the lethals was such that the

hybrid differed from either pure type. After segregation and recombination in each generation, one lethal factor killed all the individuals possessing one of the homozygous combinations, the second lethal killed the other pure type. In this way only the hybrid individuals could live; here, therefore, was a case where a hybrid type was continued from generation to generation, apparently without splitting up and forming the expected recombinations. These were formed but were killed before they could make their appearance. Such a state of affairs is rather unusual but is thought to be responsible for aberrant results in other material. It is certainly a plausible explanation of hybrid types that breed true.

Unusual segregation.—In Muller's illustration, crossing-over occurred, although rarely, between the lethal loci and the other factors carried in the same chromosome, so that a very small proportion of homozygous segregates, which lived, were obtained in each generation. How this can be possible is shown diagrammatically in Fig. 54. It must therefore be emphasized strongly that the numbers obtained in any Mendelian recombination may legitimately differ very widely from the usual expectations, and the fact that a hybrid will sometimes continue uniform without splitting is not by any means a refutation of the principles of Mendelian heredity.

Factors unfavorable to growth.—Besides the lethal factors, which stop development outright, there are many characters which hinder normal growth in plants and animals. Several different types of chlorophyll deficiency are seen in corn. At least two different factors produce plants completely lacking in chlorophyll; one of these makes pure white, the other yellow, seedlings. A third allows very small amounts of chlorophyll to be produced at the tips of the leaves. At least five other factors represent various stages of failure of the green coloring matter to develop normally. Some plants are golden in color and are weak. Other plants are striped green and white, some with

broad stripes, others with fine. All these different types, which lack chlorophyll in various degrees, are less vigorous and productive than normal plants, but when crossed with

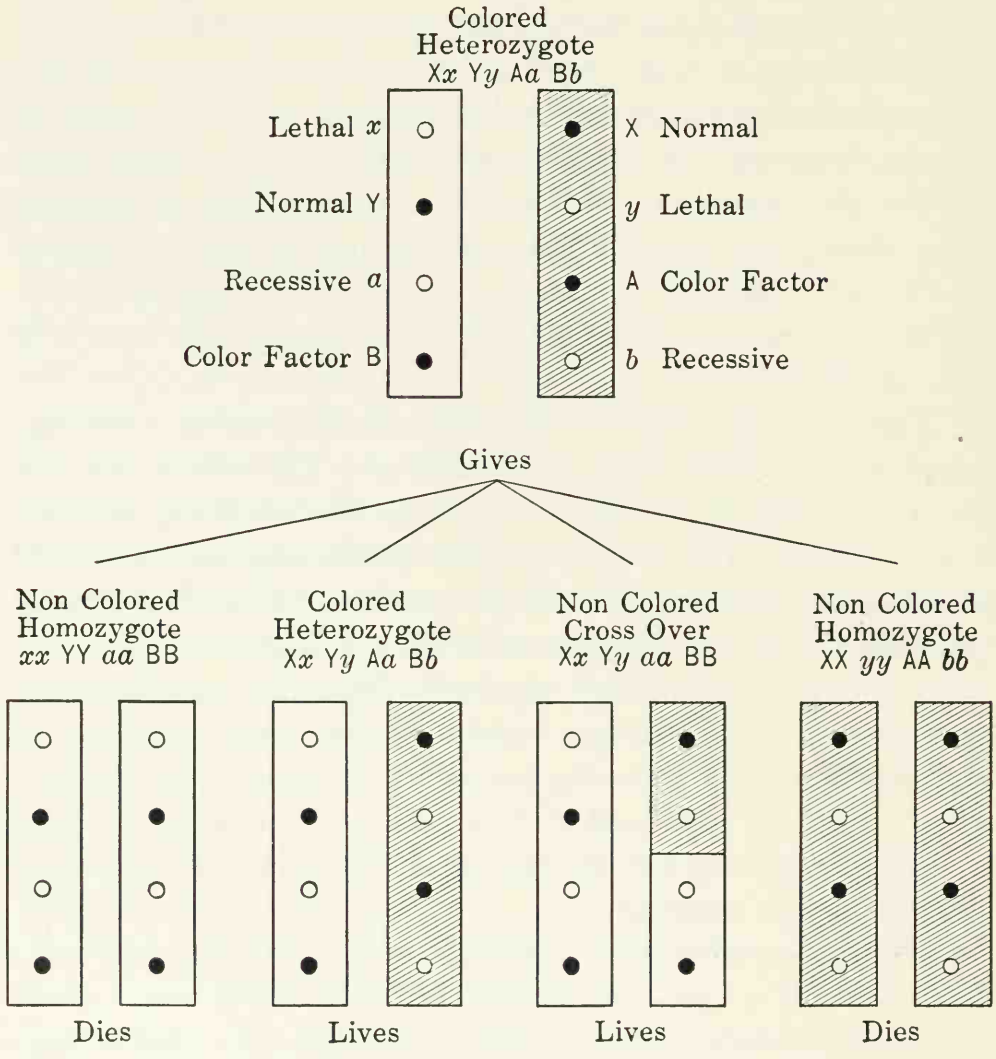


FIG. 54.—Diagram showing how balanced lethal factors may prevent the appearance of recessive characters. In this illustration two complementary color factors must both be present to produce color. One lethal factor in the homozygous condition kills all the recessives of one type, while the other lethal kills all the recessives of the other type. Occasionally, by crossing over, an individual lacking one of the color factors is produced which can live and is uncolored.

each other they give perfectly green plants with normal growth. What one plant lacks the other supplies. Other instances of deficiency in various important features are

also observed in corn. Some plants are sterile or nearly so in one or the other sex. Others are dwarf and are seldom able to grow vigorously. Some plants lack brace roots and are unable to stand upright through the season. In other plants as well, chlorophyll deficiency and sterility are commonly met with. In animals, the same general situation is found. Because these unfavorable characters are nearly always recessive, any of these deficient types, when crossed

FIG. 55.—Cross of a golden variety of corn (left), lacking in normal chlorophyll, with a dwarf race (right) lacking in normal stature. The hybrid is conspicuously taller and more vigorous than either parent.

with individuals which may be lacking in other respects, usually give normal progenies which are able to grow vigorously. An excellent illustration of this complementary action of factors is found in corn when a golden plant is crossed with a dwarf plant. Both parent types are unproductive, but this is not true of their offspring. The hybrid plants grow tall because normal stature is dominant to dwarfness. They also have green chlorophyll due to the

dwarf parent. Therefore the plants are better able to grow than either parent, and this they do. Such crosses give plants of full size and vigor, producing well-developed ears. More than just these two factors for stature and chlorophyll color are also concerned in the excellent growth of this particular hybrid. Other factors, not so distinct that they can be easily recognized and separately dealt with, are probably contributed by each parent. However, with a few illustrations which can be easily followed, it is not carrying the imagination too far to picture the whole chromosome mechanism as carrying factors, some of which are less favorable for growth than others. When contrasting factors are united, those that favor growth are dominant. This is not universally true, but quite generally so. Therefore, the progeny of two dissimilar individuals, which are not themselves hybrids, has the best of both parents to draw upon. It is therefore to be expected that in many cases hybrids will surpass either parent in growth.

Composition of cross-fertilized organisms.—Many widely crossed plants and animals are already in such a complex state of heterozygosity that further crossing does not bring together any greater number of favorable factors than they already possess. Recombinations of like factors, allowing weaknesses to appear, occur about as often, in frequent crossing among similar individuals, as the union of unlike factors. Within a variety of naturally crossed plants and in breeds of animals, therefore, growth remains on about the same level from one generation to another. When, however, two distinct types are crossed, it is quite frequently noticed that there is a decided increase in growth and vigor in the immediate progeny. Usually, the more dissimilar in visible characters are the forms united, the greater is the effect of crossing. One can cross different varieties of corn of the same general type from one locality and get very little or no acceleration of growth. But when varieties of corn from this country are crossed with types

introduced from China, as shown by Collins, very pronounced invigorating effects appear.

Because the factors which favor growth are distributed throughout the chromosomes, it is extremely difficult and in many cases practically impossible to get all the most desirable factors recombined in any one individual. Hence the best representatives in cross-fertilized animals and plants are nearly always heterozygous. When they are self-fertilized or mated with related individuals, the characters segregate. The unfavorable characters, which have been temporarily suppressed, reappear, and consequently their progeny on the average show a reduction in growth and vigor.

Here, then, is the beginning of an understanding of the injurious effects of inbreeding. A fuller discussion of hybrid vigor and the consequences of inbreeding are reserved for later chapters. Mendel's principles of heredity, together with the recently acquired knowledge of the chromosomes as the carriers of the hereditary factors, have made possible an insight into problems which have confronted man from early times.

The chromosomes and recombination.—The importance of the chromosomes in the improvement of animals and plants lies chiefly in the possibility of obtaining recombinations of desired qualities. Most of the characters with which improvement is working are complex and are probably governed by factors distributed in all the chromosomes. In practically all cases, such features as size, quality, productiveness, hardiness, and disease resistance, for which the breeder is striving, are not inherited as single Mendelian characters. To secure the highest expression of any of them, it is necessary to set out industriously to secure all the many factors regulating these qualities sought for, which may be scattered about among a large number of forms, and unite these in one superior individual. The magnitude of this task is generally underestimated. Even with 10 factors in 2 different individuals, and each located

in a different chromosome and therefore independent in transmission, it is necessary to have 1,048,576 individuals in order to run an even chance of securing in one generation the one form possessing all the desired factors in the homozygous condition. If the work is done with corn, about 75 acres of land would be needed to grow this number of plants. In practice it is never possible to secure the end sought for at once. The usual procedure is to cross several promising forms and select towards the desired goal. If sufficient numbers are employed and selecting and testing are performed diligently, there is every reason to believe the total recombination can be ultimately achieved. But with 10 factors linked together in the same chromosome, or even with some of them linked, the situation is far different. If the factors are located close together, crossing-over, which is necessary to permit recombination, may not take place except once in hundreds or even thousands of individuals.[1] Instead of the 75 acres, sufficient with the same number of factors without linkage, there would be needed an amount of land roughly 9000 million times the area of the whole United States. The difficulty would be even greater if two factors just 10 units apart were situated in each of 10 different chromosome pairs.

Distribution of hereditary factors.—Experiments prove that many characters are controlled by factors carried in all or many of the chromosomes. Especially is this true of the more complex features. In the fruit fly, wing shape, eye color and size, and body color are all affected by genes carried in all or nearly all of the chromosomes. In corn, of which the factor situation has only begun to be analyzed, there are factors for aleurone color in at least three dif-

[1] The number of individuals necessary to grow, to obtain all the recombinations on the basis of pure chance alone, can be calculated from the formula $[2(r+1)^{n-1}]^{2c}$, where $r+1$ is the linkage ratio, n is the number of factors in each chromosome and c is the number of chromosome pairs. With the example just cited, if the 10 factors are all in one chromosome and evenly placed 10 units apart, giving a linkage ratio of 9 to 1, the total number of individuals giving all combinations would be 20^{18}.

ferent chromosomes, endosperm color in two, chlorophyll production in three and endosperm texture in two. These are all distinct qualitative differences.

Productiveness, hardiness, and quality are much more complex. Yield of corn, for example, depends upon the diameter of the stalk, the number of leaves, root growth, and number and size of seeds. These in turn are governed by the rate of cell division and the general growth activity of the entire plant. No one has as yet adequately analyzed the individual factors concerned in these processes. Resistance to disease and ability to withstand unfavorable climatic conditions involve the chemical and physical structure of the cells, and the thickness and texture of the epidermis, among other things. Quality, that illusive something so generally desired, is even more intricate. In sweet corn, for example, one must take into consideration the amount of sugar, thickness of the pericarp, structure of the cell walls, and rate of maturity, as well as chemical composition in substances about which very little is known.

Recombination and the number of chromosomes.—Since the factors governing the characters with which the plant and animal breeder are chiefly concerned are distributed throughout the chromosomes, the difficulty in the improvement by hybridization usually depends upon the closeness with which the factors are linked. The chance of two contrasting factors being transmitted together or separately is always equal in independent segregation, whereas with linkage the number of breaks in the association of factors is usually very much less than equality. For example, in sweet peas the disjunction of purple flower color and erect petals occurs only about once in every 128 times. In corn, the factors for red aleurone color and golden chlorophyll separate once in every four gametes on the average, but the separation of the same aleurone color factor and the yellow seedling chlorophyll factor has not yet been observed. But as the factors are farther and farther apart, the facility with which they disunite and go into new combinations

TABLE VIII

CHROMOSOME NUMBERS REPORTED BY VARIOUS INVESTIGATORS FOR SOME OF THE COMMON PLANTS AND ANIMALS

Common Name	Classification	*N*	2*N*	Investigator
Plants				
Bean	*Phascolus vulgaris*	8	16	Wager
Calla lily	*Richardia Africana*	8	16	Overton
Corn	*Zea Mays*	10–12	20–24	Kuwada
Cotton	*Gossypium* " hybrid "	28	" 56 "	Cannon
Cotton	*Gossypium* " Egyptian "	20	..	Balls
Currant	*Ribes* 2 sp.	8	" 16 "	Tischler
Elderberry	*Sambucus* sp.	18	38	Lagerberg
Evening primrose.	*Œnothera grandiflora*	7	14	Davis
Evening primrose.	*Œnothera lamarckiana*	7	14	Gates
Evening primrose.	*Œnothera gigas*	14	28	Gates
Fern	*Nephrodium molle*	64 or 66	128 or 132	Yamanouchi
Flag	*Iris squalens*	12	24	Strasburger
Pea	*Pisum sativum*	7	14	Cannon
Pine	*Pinus laricio*	12	24	Chamberlain
Rice	*Oryza sativa*	12	24	Kuwada
Rose	*Rosa* sp.-3 species	8	16	Strasburger
Tobacco	*Nicotiana* sp.	24	48	White
Tomato	*Solanum lycopersicum*	12	24	Winkler
Tulip	*Tulipa Gesneriana*	12	24	Ernst
Wake-robin	*Trillium Grandiflorum*	6	12	Atkinson
Wheat	*Triticum monococcum*	7	14	Sax
Wheat	*Triticum dicoccum*	14	28	Sax
Wheat	*Triticum vulgare*	21	42	Sax
Animals				
Artemia	Crustacea	84	168	Brauer
Ass	Mammals	32	64	Wodsedalek
Dog	Mammals	11	22	Malone
Earthworm	Annelids	16	32	Calkins
Fowl	Birds	9	18	Guyer
Frog	Amphibia	12	24	Von Rath
Guinea pig	Mammals	8	16	Bardeleben
Horse	Mammals	19	38	Wodsedalek
Man	Mammals	24	48	Von Winiwarter
Monkey	Mammals	27	54	Painter
Mouse	Mammals	12	24	Sobotta
Ox	Mammals	8	16	Bardeleben
Rat	Mammals	8	16	Moore
Thread worm	Nematodes	1	2	Van Beneden
Sea urchin	Echinoderms	9	18	Boveri

increases. The number of breaks in the linkage of two factors lying in the same chromosome, expressed as percent of the gametes formed, is taken as a measure of the distance

between them. One percent crossing-over is the unit of distance. When the space between two loci is 50 units or more, these points separate as often as they go together. In other words, they are as independent of each other in transmission as two factors which are in different chromosomes. Therefore, the number of chromosomes characteristic of the species is not as important as the number and arrangement of the factors in the chromosomes. Plants and animals differ considerably in number of chromosomes. Some species of roses have 8, corn 10 or 12, tobacco 24, and cotton 20 to 28 pairs. The rose,with its 8 chromosomes, seems as complex in its hereditary make-up as cotton, with 20 or more, and presumably has as many transmissible factors The difficulty of recombination depends not so much on the number of chromosomes as upon the number of 50-unit lengths, that is, the amount of chromatin. Linkage, however, is not altogether a hindrance, as when desired factors are once recombined they tend to stay together just as strongly as they before resisted separation. In this manner the advantageous and disadvantageous effects of association of factors in the same chromosomes tend to balance each other.

Summary.—The recently acquired knowledge of the chromosomes as the carriers of the inheritance has advanced the study of heredity considerably beyond the stage at which Mendel left it. The segregation and the recombination of unmodified determiners, which are the most important principles set forth by Mendel, still hold true. The way inherited qualities are handed on from one generation to the next is now more clearly understood. The practically universal use of the chromosome mechanism by all forms of life is indicated. Hybrid types, which sometimes breed true as well as aberrant segregating forms, are better understood, and instead of refuting Mendel's principles are valuable evidence in support of them. The injurious results of inbreeding and the converse benefit from crossing are more readily accounted for when considered with the

chromosomes as the carriers of the inheritance. The possibilities of obtaining valuable associations of characters depend very largely upon the arrangement of the determiners in the chromosomes, and when this is known some realization can be had of the number of individuals necessary to work with.

CHAPTER VI

SEX AND SEX-LINKED CHARACTERS

It is a matter of common observation that the two sexes of the higher animals are born in approximately equal numbers. Many theories have been advanced to account for the determination of sex, and some have seemed to offer a means of changing the ratio of the two groups. Most of these theories are merely crude guesses seemingly supported by statistics, which are not based upon numbers large enough to be authoritative. One of the oldest of these surmises is that the time of year at which birth takes place influences the sex of the offspring. Small differences have been found in the sex-ratios of young classified in this way, but the results do not agree on any particular time which favors either sex. Probably the most commonly heralded opinion is that the amount or kind of food supplied to the mother influences the sex of the forthcoming offspring. In general, a favorable nutritive condition is supposed to increase the production of females. This has been extensively investigated, with the result that an excess of males is obtained as often as the reverse. Furthermore, it has been found that neither the vigor nor the age of the male or female parent has any consistent connection with the sex of the offspring, although in some animals more male than female offspring are still-born from aged female parents.

Cattle breeders frequently maintain that the time of service in relation to the beginning of heat determines the sex, and that early service tends to produce females whereas a greater proportion of males result from service late in heat. Pearl and Parshley at the Maine station have

gathered extensive figures bearing upon this; and while the data first gathered indicate that there might be such a relation, later results show no significant differences. A theory often proposed, without any justification whatever, is that the germ cells from one of the two sex glands in the male determine one sex and those from the other gland the opposite sex. Alternative to this is the theory that the ova from one ovary result in females and those from the other in males. The hospital records which report births following the removal of one or the other gonad are sufficient to disprove this contention. The numerous direct experiments which have been performed on domestic animals and rodents also demonstrate convincingly that there is no foundation for such a belief. Moreover, there is naturally only one functional ovary in birds.

The evidence from multiple births.—Many animals give birth to large numbers of young at one time, and among these simultaneous offspring the sexes are distributed at random. From this it should be evident that the ordinary influences of the environment, such as food and season, can have no effect, since these external conditions are alike for all the offspring in any one litter. In man, twins are of two kinds: those which differ as much as any children born at separate times and which may be of the same or opposite sex; and those which are remarkably alike in all their features and mannerisms. The former are known as fraternal twins, the latter as identical twins. Fraternal twins result from the simultaneous production of two ova and their fertilization by two separate sperms. Identical twins, upon reliable evidence, result from the division and separation of the halves of one ovum shortly after fertilization. Thus identical twins have exactly the same set of chromosomes with their hereditary factors. They are invariably of the same sex. A similar result regularly occurs in the nine-banded armadillo, where one fertilized egg cell produces four identical quadruplets, alike in sex as well as in all other observable characters. This indicates that sex is con-

trolled in much the same way as are other hereditary characters and is as well insulated from external influences.

Chromosome differences associated with sex.—Soon after methods of preparing and staining tissue sections for microscopical examination were developed, several cytologists noted that half of the spermatozoa of certain insects contained one more chromosome than the other half. McClung, in 1902, suggested that this odd chromosome in some way was associated with the differences in sex. The ova were all alike in number of chromosomes, and it was suggested that those which were fertilized by one kind of sperm developed into males while the other combination produced females. This subject was extensively investigated by Wilson, Stevens, McClung, and others, and it was discovered that inequality of the germ cells in chromosome content was comparatively common in many different animals, including, besides insects, echinoderms, nematodes, mollusks, and vertebrates such as birds and man.

As an illustration, it is known that the grasshopper has 13 chromosomes in the body cells of the male. These comprise 6 evenly paired chromosomes and 1 unpaired chromosome. The female has 14 chromosomes, all of which are evenly paired. Six of these pairs are similar in size and shape to the 6 paired chromosomes of the male. The remaining pair in the female are like the 1 odd chromosome in the male. At the reduction division, in the process of forming the reproductive cells, the 14 chromosomes of the female come together in matched pairs and then separate, 7 going into one daughter cell and 7 into the other. In the male the 6 pairs and the 1 odd chromosome arrange themselves in order and separate. The odd chromosome does not divide but goes intact into one of the two daughter cells. Therefore, half of these cells contain 7 chromosomes, like all the egg cells, while the other half contain only 6 chromosomes. This is shown diagrammatically in Fig. 56.

At fertilization, the two types of sperm unite at random with the one type of ovum and produce fertilized eggs, half

of which contain 14 chromosomes and develop into females, while the others have only 13 chromosomes and develop into males. By this mechanism the determination of sex becomes a matter of chance at the time of fertilization.

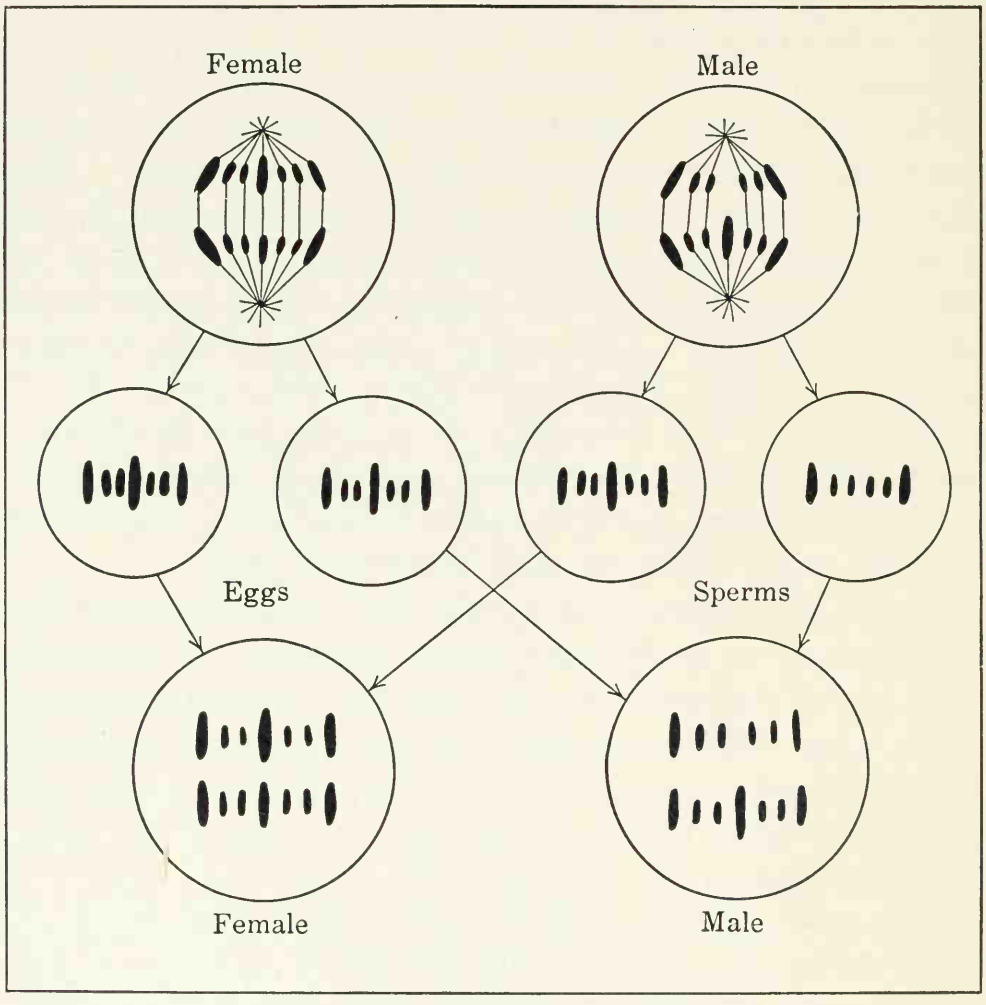


FIG. 56.—Diagram illustrating the method of sex-determination in an animal with 14 chromosomes in the cells of the females, 13 in the males. All eggs have 7 chromosomes, but only half the sperms have 7 chromosomes, the other half having 6. The former are female-determining sperms, the latter male determiners. (After Wright in U. S. Dept. Agr. Bull. 905.)

Possibility of controlling sex.—A means of controlling the production of either sex lies in the possibility of separating or changing the relative amounts of the two kinds of sperm cells and artificially impregnating with the type of sperm which produces the sex desired. This is a possibility

only, as up to the present time no method has been developed by which either of these results can be satisfactorily accomplished.

Variation in chromosome differences.—In some animals, the difference in chromatin content is not due to the lack of one chromosome but rather to the unequal size or shape of one of the chromosome pairs. This occurs in some species of Drosophila, as represented in Fig. 57. As previously stated, the 4 chromosome pairs of this insect are charac-

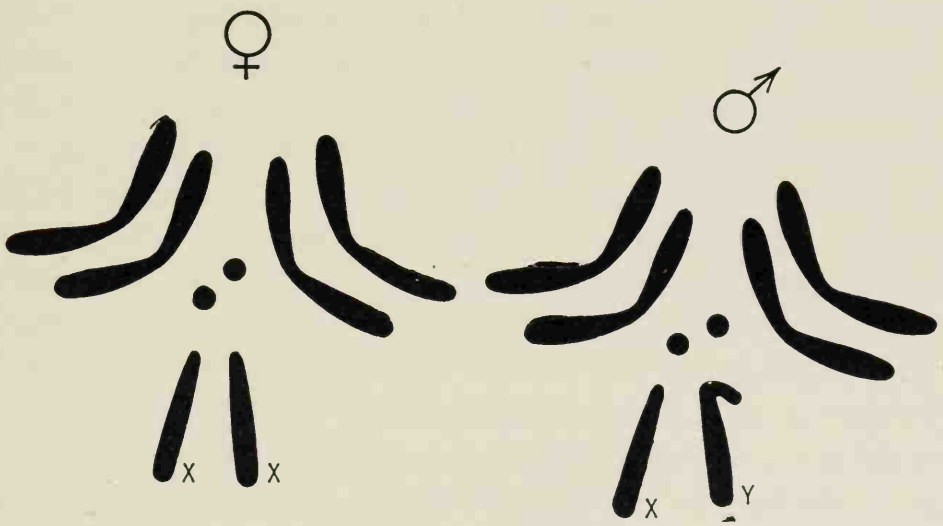


FIG. 57.—Diagram of female and male group of chromosomes of *Drosophila melanogaster* showing the four pairs of chromosomes. The Y chromosome is not always formed as shown here. The members of each pair are usually found together. (After Morgan *et al.* in "Mechanism of Mendelian Heredity," courtesy of Henry Holt & Co.)

teristically formed. Three of them are equally paired in both sexes, but in the male the simple rod-shaped chromosome has a mate which is different. The shape of this odd chromosome varies considerably and it can not always be identified. It has been proved, from several sources of evidence, that this pair of chromosomes are concerned with the determination of sex. They are called the sex chromosomes, the one which is evenly paired in the female being designated as the X chromosome and the odd one as the Y chromosome. Normally, every individual with one Y and

one X chromosome is a male, and every individual with two X chromosomes is a female. The male in this case therefore determines the sex. Since he has unlike chromosomes the male is *heterozygous,* while the female is *homozygous* for *sex.*

Operation of the chromosome mechanism of sex determination.—It should be noted that the production of the two sexes corresponds to the back-crossing of a heterozygous Mendelian pair of factors with the homozygous recessive. Two types are produced in equal numbers. Since there is no way, normally, by which two Y chromosomes can come together, the heterozygous male condition is continually perpetuated and the mechanism works in such a way as to produce the two sexes in approximately equal numbers.

No differences can be seen under the microscope in any of the chromosome pairs of some animals, but it is assumed that some one pair is primarily concerned with sex, just as in those forms in which a visible difference can be discerned. Since other hereditary factors are carried by the sex chromosomes, as will be shown later, the assumption is that a definite sex factor or factors exist, located somewhere on the sex chromosome. When two doses of these sex determiners are present, femaleness results. With only one dose, the outcome is maleness. The Y chromosome in many species is missing and in most of the others apparently carries no effective hereditary determiners. In certain species of fish, factors have been located in the Y chromosome. The characters that result are transmitted only from father to son. In Drosophila the Y chromosome, although normally present, may be missing in certain aberrant cases, and such individuals are visibly males but are sterile. Apparently the Y chromosome has some function in those species in which it occurs, but its importance is not fully understood. With the exception of one animal, the fish, there is no crossing-over in the sex chromosomes of the male, and it has so far been impossible to determine the location of the sex-governing factor or factors in the sex chromosomes.

Chromosome aberrations.—The hypothesis that sex is controlled by the chromosomes, and is transmitted from generation to generation by the same mechanism that distributes the hereditary factors, receives its strongest confirmation from a series of results which follow the abnormal behavior of the chromosomes in Drosophila in certain cases, as worked out by Bridges and confirmed by others. It has been shown cytologically that on rare occasions the 2 X chromosomes fail to separate at the reduction division and both pass into one egg cell, leaving none in the other. When these abnormal eggs are fertilized by ordinary sperm cells, various types of exceptional offspring result that are not expected by the usual method of transmission of factors carried in the sex chromosomes. Other offspring are produced which are not themselves unexpected but which give exceptional offspring in the next generation. It has been shown beyond doubt that this unusual transmission of hereditary characters follows exactly the abnormal distribution of the sex chromosomes.

The same failure of the sex chromosomes to separate as usual may also occur in the body cells of a developing animal, as has been demonstrated in Drosophila. Such individuals show features of both sexes. Males and females in Drosophila differ in many respects throughout the entire body. Some have been obtained which have the external features of the male on one side of the body and of the female on the other. When such a **gynandromorph** is also heterozygous for a character which is carried in the X chromosome, such as yellow body color instead of the normal gray body, that part of the fly which has the features of the male may have the recessive, yellow coloration. The female part always has the dominant color whenever there is a difference of this kind. The evidence is clear that at an early cell division one of the two X chromosomes of an individual which would normally have been a female did not divide properly, so that part of the cells contained only one X chromosome whereas the other cells contained

three. The association between the sexual features and the body color can only occur when the chromosome with the recessive character is left unpaired. Such an occurrence is extremely rare, but enough of these abnormal flies have been obtained to demonstrate conclusively the parallel between chromosome distribution and sex.

Characters more frequently associated with one sex.—Other evidence bearing upon this problem has been known for a long time but was not clearly understood until the chromosome theory of sex determination was developed. It was first pointed out in 1820, in the case of **hemophilia,** an abnormal hereditary condition in man whereby the blood fails to clot properly and excessive bleeding follows even minor injuries, that the affliction is more common in males than in females. Curiously, this abnormality is not transmitted from father to son, and neither does it reappear in the son's descendants. The daughters of an affected male, while themselves normal, transmit hemophilia to half of their sons on the average. This singular mode of inheritance could not fail to attract attention but was a complete mystery until the chromosome theory fully explained it. It will be seen that this peculiar distribution is exactly what would be expected if the hereditary trait is recessive and determined by a single factor located in the sex chromosome.

Sex-linked characters.—Many other characters, in man and in other animals, are inherited in the same way. Such traits, the determiners of which are located in the X chromosome and parallel the distribution of sex, are called **sex-linked** characters. They are sometimes erroneously called sex-limited characters. They are not limited to either sex, but they always appear more frequently in the heterozygous sex.

Inheritance of color blindness.—This is made clear in Fig. 58. Color blindness, the inability to distinguish properly between red and green, is a sex-linked character. When a color-blind male is mated with a female having the dominant factor for normal color perception in both X

chromosomes, the children of either sex are normal. All of the daughters, however, carry the recessive trait. When the daughters marry men of normal vision, half of the grandsons are color blind, whereas none of the grand-

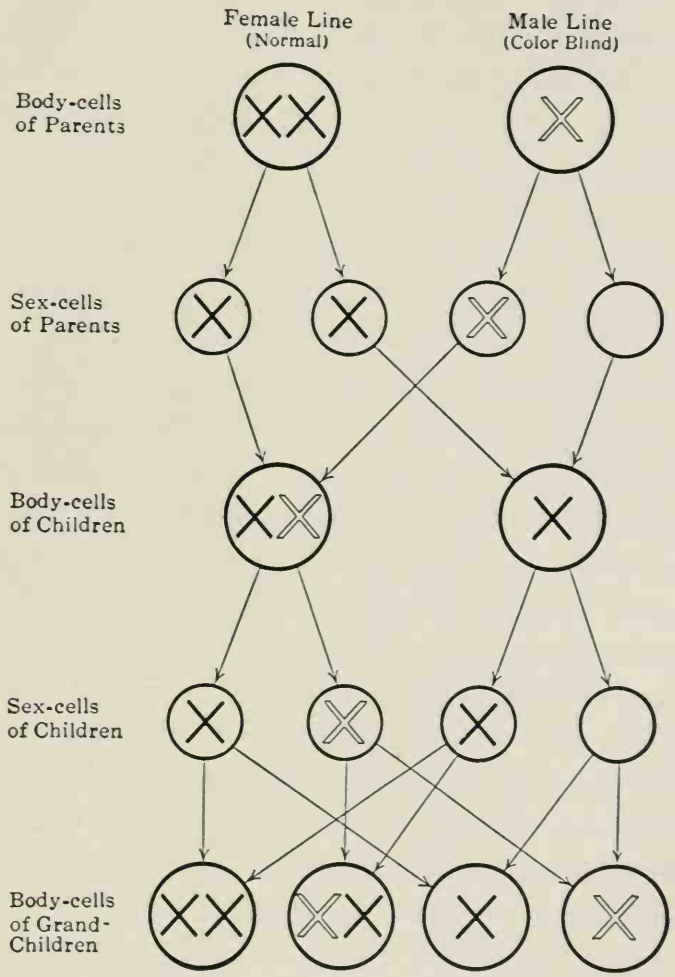


FIG. 58.—Diagram illustrating the transmission of a sex-linked character, such as color blindness in man. The normal sex chromosome is indicated by a black X; the one lacking the factor for color perception by a light X. It is assumed that a normal female is mated with a color-blind male. (After Guyer in "Being Well Born," courtesy of Bobbs-Merrill Co.)

daughters are, although half of them will still carry the factor for color blindness. When such heterozygous females are mated with color-blind males, half of the daughters as well as half of the sons will, on the average, have the defective vision.

Since color blindness and similar recessive abnormalities are comparatively rare in the general population, it is very unusual for an afflicted male to mate with a female heterozygous for the same abnormality. Therefore, females showing sex-linked characters are rare.

Tortoise-shell cats.—Yellow coat color in cats is another example of an hereditary factor located in the sex chromosome. When a yellow cat is crossed with black, neither color is dominant but both are mixed in a mosaic pattern which is commonly called tortoise-shell. Representing the chromosome that carries yellow as Xy, and the one carrying black as Xb, the three kinds of females with respect to these two color factors are (XyXy) yellow, (XbXb) black, and (XyXb) tortoise-shell. There are commonly only two kinds of males, yellow (Xy−) and black (Xb−), and this is to be expected since they have only one X chromosome. It is well known that tortoise-shell males are so rare as to be classed as freaks. They are practically always sterile and are probably the result of chromosome aberrations similar to those described above, occurring in Drosophila.

Females heterozygous for sex.—While the evidence furnished by the microscope and by breeding experiments proves conclusively that in many animals it is the male that is heterozygous for sex, it is equally clear that in certain other animals it is the female that has the unevenly paired sex chromosome. Those animals of which the males are known to produce two kinds of germ cells are flies and grasshoppers among the insects and, in the vertebrates, the dog, cat, pig, cow, horse, and man. Other insects, the moths, have the heterozygous chromosome in the female. This is a condition which is exactly the reverse of that in flies and grasshoppers. Also with birds, including poultry, the female produces two classes of gametes and determines the sex.

Types of sex-linked inheritance.—In sex-linked inheritance the results of various matings differ according to whether the dominant factor comes from the heterozygous

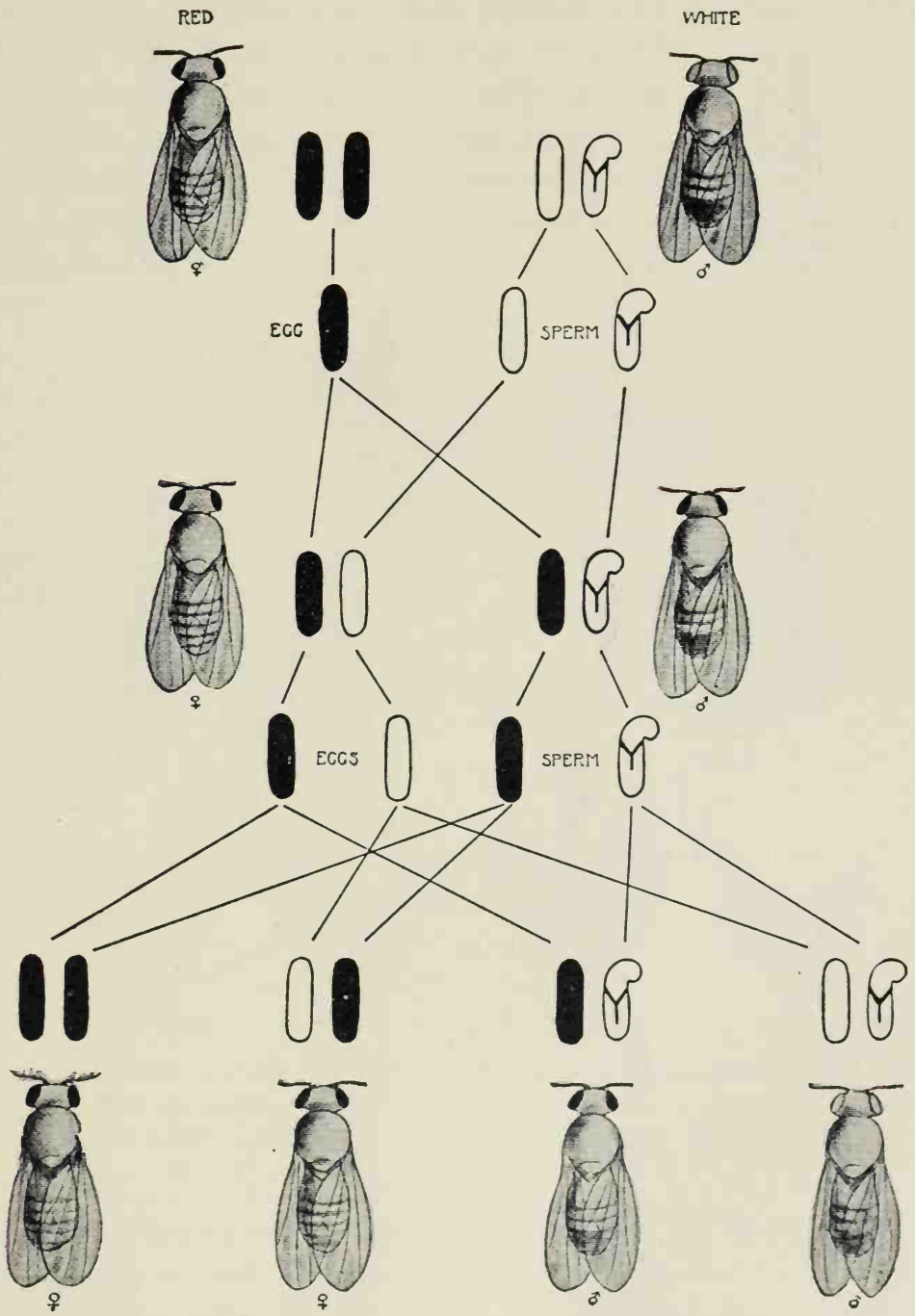


FIG. 59.—The result of crossing a white-eyed male (*Drosophila melanogaster*) and a red-eyed female. The first generation all have red eyes, as have all the females of the second generation, while half the males of this generation have white eyes like their grandsire. The reciprocal of this cross is shown in Fig. 60. (After Morgan *et al.* in "Mechanism of Mendelian Heredity," courtesy of Henry Holt & Co.)

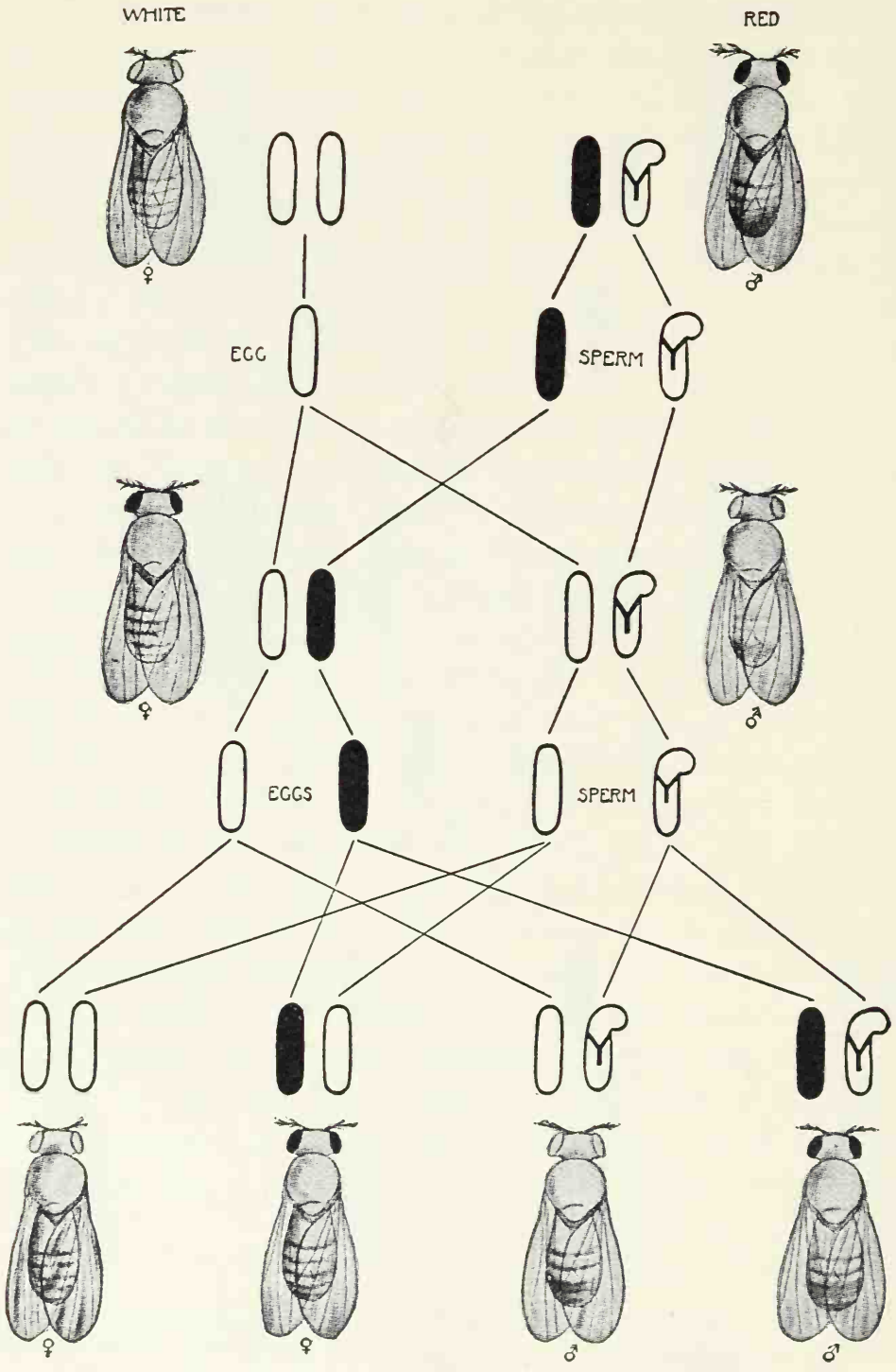


FIG. 60.—The result of crossing a red-eyed male and a white-eyed female. All daughters in the first generation have red eyes like their father while all the sons have white eyes like their mother. In the second generation both colors are reproduced in both sexes in equal numbers. (After Morgan *et al.* in "Mechanism of Mendelian Heredity," courtesy of Henry Holt & Co.)

or the homozygous sex. This is shown for the Drosophila type of sex determination in Figs. 59 and 60. Some thirty or more genes have been located in the sex chromosome of the fruit fly. Among these the recessive white eye color contrasted to the normal red eye is one of the most useful characters to demonstrate sex-linked inheritance. As diagrammed in Fig. 59, where a white-eyed male is mated with

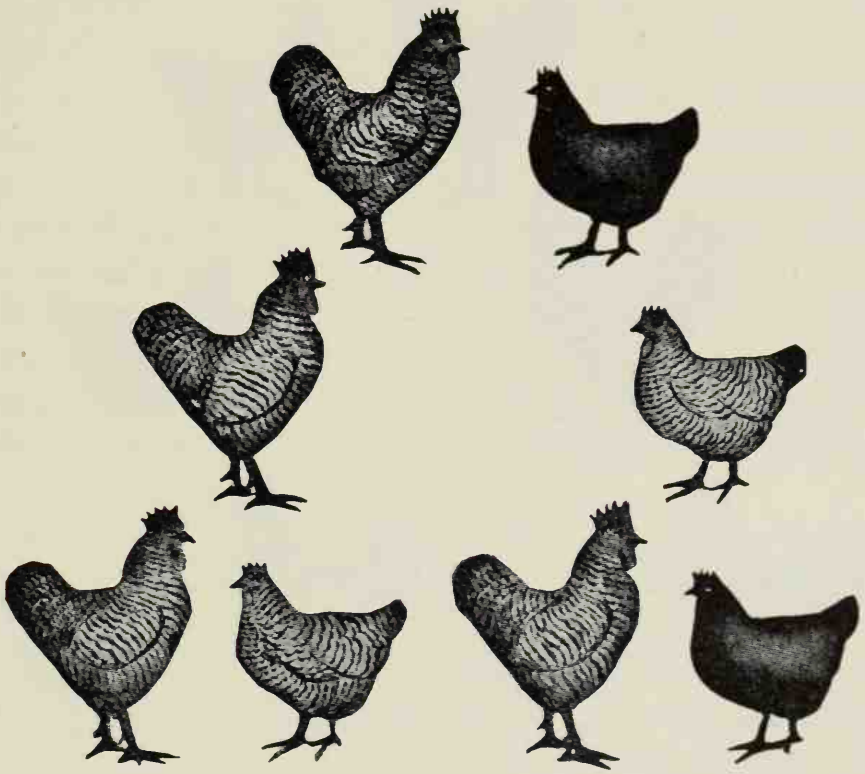


FIG. 61.—Black Langshan female by Barred Plymouth Rock male. The result is the same as shown in Fig. 59 except that the sexes are reversed. (After Morgan *et al.* in "Mechanism of Mendelian Heredity," courtesy of Henry Holt & Co.)

a pure-breeding red-eyed female, all of the offspring of both sexes in the first generation have the dominant red color. When these are bred together it will be found that all of the females are red-eyed in the next generation while half of the males are red and half are white. This is easily understood by following the distribution of the X and Y chromosomes, remembering that the Y chromosome is inactive as far as the hereditary factors are concerned.

When the reciprocal cross of red-eyed male with white-eyed female is made, the result is quite different. All the first-generation males have white eyes like their mother, and all the females have red eyes like their father. The transmission takes place in a criss-cross manner. Breeding

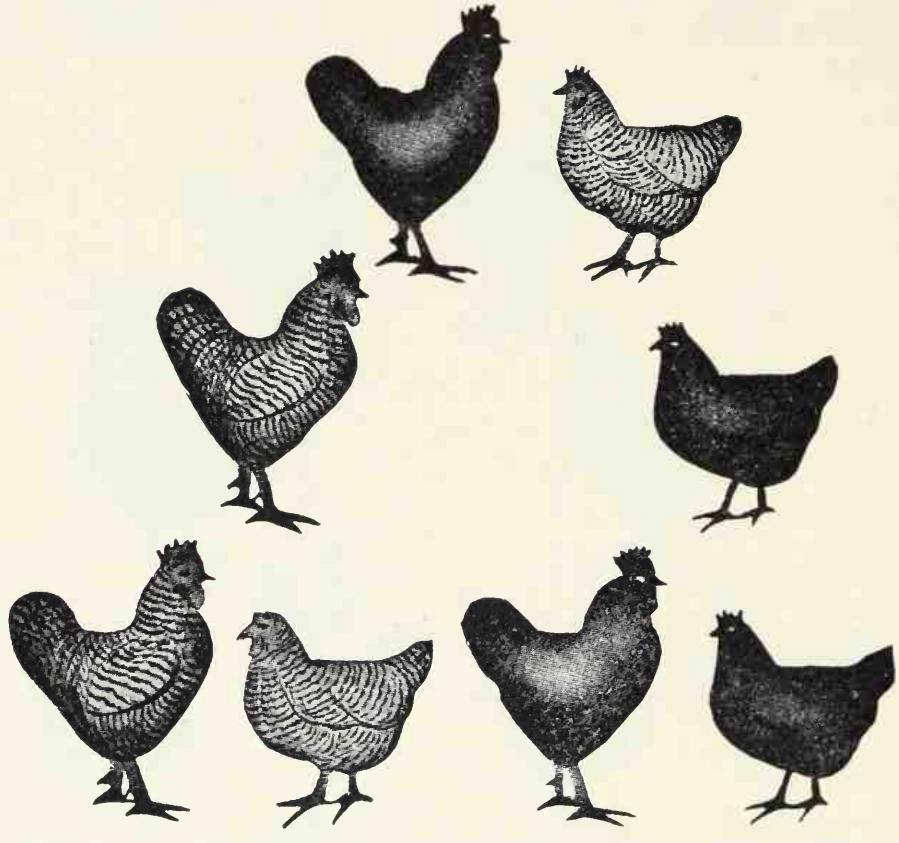


FIG. 62.—Barred Plymouth Rock female by Black Langshan male. The result is the same as shown in Fig. 60 except that the sexes are reversed. (After Morgan *et al.* in "Mechanism of Mendelian Heredity," courtesy of Henry Holt & Co.)

these individuals with each other gives both red- and white-eyed males and females in equal numbers.

In birds, the situation is similar except that the sexes are reversed, as shown in Figs. 61 and 62. When a barred cock is mated with a black hen, all the offspring of both sexes are barred since the factor for barring is dominant over solid color. The next generation gives 1 black to 3 barred, and the sex of the recessive individuals is always the

same as that of the grandparent with the recessive character. The reciprocal combination of black cock and barred hen gives the criss-cross inheritance in the first generation, followed in the second generation by the production of all four classes with respect to sex and plumage pattern in equal proportions.

Rules for sex-linked inheritance.—From this series of facts the following rules governing the transmission of sex-linked characters can be deduced.

1. When the **homozygous** sex transmits the **dominant** factor, all of the offspring in the first generation exhibit the dominant character and the second generation is composed of three dominants to one recessive, the latter having the same sex as the recessive grandparent.

2. When the **homozygous** sex transmits the **recessive** factor, both dominant and recessive characters are exhibited in the first generation, but exclusively upon the opposite sexes, and in the second generation both sexes show the sex-linked characters in equal numbers.

Sex-limited characters.—There are certain characters which may be shown in one sex but never in the other, or certain features may be more intensified in one sex than in the other. This is well illustrated in birds, where the comb and spur development, type of plumage, and coloration of the males is more extreme than in the females. Such differences, which are always associated with one sex, are called **sex-limited** characters. Since sex-linked factors can be transferred to either sex, these sex-limited characters must be governed in some other way than by factors carried in the chromosomes. From experiments in which the sex glands have been removed and replaced by those of the opposite sex it is apparent that sex-limited characters are due to some influence exerted by the sex glands themselves, and brought about by substances, called **hormones,** secreted by them and introduced into the blood. The recently discovered characters governed by factors carried in the Y chromosome, previously mentioned, which have been

reported independently by Aida, Schmidt, and Winge, are also limited to one sex. They are, however, essentially sex-linked characters as they have their basis in the chromosome mechanism, as do sex-linked characters which may appear in either sex.

Castration experiments with poultry.—In an extensive series of investigations with poultry, Goodale and Morgan have shown that the differences in plumage between males and females is largely due to the influence of the ovary. With the ovaries entirely removed, the pullet takes on the feathering of the cockerel. The inconspicuously colored Rouen duck assumes the brilliant colors of the male, following the next molt, when similarly treated. A hen whose ovaries had been destroyed by a tumor was shown by Cole and Lippincott to develop plumage which resembled the typical male or capon. When a piece of ovary from a normal hen was introduced into the body cavity of the same hen, normal female feathering was brought back. Cockerels have been feminized in external appearance by Goodale by castrating them and engrafting ovaries.

Characters both sex-limited and sex-linked.—Another type of sex-limited inheritance is produced by factors which are carried in the chromosomes and distributed to either sex, but which can only appear in one sex. Characters governed by such factors may be both sex-linked and sex-limited. Pearl has found that one of two main factors which are necessary for high winter egg production, in Barred Plymouth Rock hens tested at the Maine Station, is carried in the sex chromosome and is therefore sex-linked. Since egg production is exclusively a function of the female, the factor is also sex-limited. However, it may be that factors of this kind, controlling egg laying, may also affect the production of male germ cells as well, and in that case would not be strictly limited to either sex.

The two sexes not formed in equal numbers.—The view that sex is determined at the reduction division, when two classes of gametes, one male-producing, the other female-

producing, are formed in equal numbers by one or the other sex, indicates that the two sexes should be exactly equal in numbers, on the average, provided that there are no other complicating influences. Statistics show that the sex ratio varies significantly from equality in different animals. The following figures have been compiled by Morgan for the common animals:

	Males	Females	Authority
Horse	98	100	Düsing
Cattle	107	100	Wilckens
Sheep	98	100	Darwin
Pig	112	100	Wilckens
Rat	105	100	Cuénot
Pigeon	105	100	Cole
Dove	105	100	Cuénot
Fowl	95	100	Darwin

The most extensive figures have been compiled for man, with the result that the ratio ranges from 104 to 108 males for every 100 females. When the still-born and abortive births are taken separately, the ratio is much higher, ranging from 125 to 142 males for every 100 females and in some cases even above this. There can be no doubt that in some animals more male than female embryos are regularly initiated and that the male embryo is less viable than the female.

The reason for the greater production of males than females is not clear. Morgan suggests the possibility that the smaller size of the male-determining sperm, due to the fact that it has one less chromosome, may make it more active and somewhat better able to reach the egg and accomplish fertilization. A slight constant difference in this respect would probably affect the sex-ratio, but this explanation does not apply to those species in which no differences in amount of chromatin is apparent. Moreover, in birds, the females should be in excess according to this theory.

Influences which modify the sex-ratio.—There are many things which may modify the sex-ratio among the living offspring, but they are due to causes which have nothing to do with sex-determination in the first place. Lethal factors, which stop development shortly after fertilization or at early stages of growth, are more effective in eliminating the heterozygous sex, since with only one X chromosome any recessive factors carried by that chromosome can not be masked by their dominant allelomorphs. In many experiments with Drosophila and other animals in which the males are heterozygous for sex, it is not uncommon to get ratios of two females to one male, half of the males being eliminated by lethal factors.

Wide crossing frequently results in distorted sex-ratios.—Males result infrequently from crossing the bison and the cow. Detlefsen obtained a low proportion of males in crosses of wild and tame guinea pigs. The ratio became more nearly equal as the hybrid animals were bred back in successive generations to tame guinea pigs, as shown in Table IX. On the other hand, wide crosses among birds give abnormally high ratios of males to females. This

TABLE IX

RATIOS OF THE SEXES IN HYBRID GUINEA PIGS

Data from Detlefsen, in Carnegie Institute Publication No. 205

Generation	Males	Females	Total	Number of Males to 100 Females
F_1, $\frac{1}{2}$ wild	14	23	37	60.87
F_2, $\frac{1}{4}$ wild	31	52	83	59.62
F_3, $\frac{1}{8}$ wild	101	116	217	87.07
F_4, $\frac{1}{16}$ wild	159	153	312	103.92
F_5, $\frac{1}{32}$ wild	173	171	344	101.17
F_6, $\frac{1}{64}$ wild	58	64	122	90 63
F_7, $\frac{1}{128}$ wild	16	21	37	76.19
Total	552	600	1152	92.00

shows the close parallel that exists between the behavior of the sexes in relation to the chromosome condition.

Sex-ratios in lower animals.—Quite variable results are obtained with many of the lower animals. At certain times or under particular conditions, all of the offspring may be of one sex. The production of either sex may be altered by external conditions, such as the kind and amount of food given, temperature, and age of sperm or eggs at the time of fertilization. In most of these cases the animals have the ability to produce young from unfertilized eggs. Such parthenogenetic individuals may be entirely of one sex. When the eggs are fertilized the other sex is produced. This is the case with bees and other insects, where the unfertilized eggs produce drones, the males, and the fertilized eggs develop into sterile females, the workers, or fertile females, the queens. Since in the higher animals fertilization is indispensable, the results so far obtained from the lower forms of life do not offer any means of controlling sex in domesticated animals.

A physiological conception of sex determination.—An entirely different theory of sex determination has been proposed by Whitman and Riddle. From their experiments with doves they are convinced that sex, in these animals at least, is not entirely a matter of chance at the time of fertilization, due to the random union of gametes carrying different sex determiners. They believe that sex is controlled by the animals themselves to a certain extent and is also influenced by external conditions. The dove regularly lays two eggs for a sitting. Their observations seem to show that the first egg laid more often hatches into a male and the second into a female. The yolk of the first laid, male-producing egg, according to Riddle is smaller and has a lower content of stored food than the second or female-producing egg. Riddle states that it is possible to reverse the sex by treating the eggs in such a way as to change the amount of stored food, water content, and growth activity. In his opinion, sex is not dependent upon distinct, qualita-

tive, mutually exclusive differences in the germ cells, but is a quantitative and modifiable character. According to this conception, the two sexes represent two levels in a continuous series of a growth process that may pass from one condition into the other during the early stages of development.

This view of sex can not be reconciled at present with the cytological evidence and the results from breeding experiments, and has been subjected to much destructive criticism. Cole and Kirkpatrick have shown that in the pigeon, a closely related bird, the sexes of the two squabs from the same clutch are distributed wholly at random. In doves, moreover, the order in which the eggs are laid is not completely correlated with the type of sex, and Wright states that the departures from a random distribution obtained by Whitman and Riddle are not positively significant.

Sex modified by internal secretions.—There is evidence, from a peculiar phenomenon in cattle, that sex can be modified. When twins of both sexes are produced simultaneously, the female calves are regularly sterile. They are called free martins, and examination of their internal organs shows that these have been changed into partially developed male organs. It is assumed in this particular case that the secretions from the sex glands of the male embryo are able to bring about this transformation. This indicates that sex is not irrevocably fixed at the time of fertilization. However, there is no positive case in cattle in which an individual having the chromosome content of one sex has been completely changed into the opposite sex and has been able to function normally. Moreover, there is considerable question as to the condition of such individuals with regard to health and vigor, granting that they could be produced; so that, for practical purposes, no method has yet been found whereby sex can be controlled.

A remarkable case of sex reversal has been reported by Crew to have occurred in Scotland. A hen, which had laid eggs and hatched chicks from them, later gradually

took on the appearance and behavior of a male. A post-mortem examination showed that the ovary was practically completely destroyed by a tumor due to tuberculosis. Similar changes to masculine characters have been observed in numerous instances in different kinds of poultry. The unusual feature of this case was that the bird developed testes and functioned as a male bird, becoming the " father " of two chicks. One of these proved to be a male, the other a female. When mated they produced normal offspring, typical of the breed to which their peculiar grandparent belonged.

Sex-ratio modified by hereditary factors.—Opportunity does lie in the fact that the ratio of the two sexes can be altered somewhat by hereditary factors. Miss King, at the Wistar Institute, has demonstrated with rats that the proportion of males to females can be regularly increased or decreased by selection. The normal ratio in rats is approximately 105 males to 100 females. Working with large numbers and continuously breeding from families which produced a large excess of males, she was able to establish a strain that averaged 122 males to 100 females. In the opposite direction, a strain was obtained with an average production of 82 males. How this difference is brought about is not known. According to the chromosome theory of sex determination, the X and Y types of gametes must be produced in varying numbers, subject to control by transmissible factors, or else fertilization is not wholly at random but selectively influenced in some way. Whether or not these results can be duplicated in other animals can not be stated, nor is it evident that such differences would be worth the time and effort probably necessary to obtain them.

Fluctuations in sex-ratio.—Although inequality in the distribution of the two sexes in single families may be due in part to hereditary differences, ordinarily it is merely the outcome of chance allotment. Dairymen are often dissatisfied with a bull which produces a large number of male

calves. It should be remembered that if a coin is tossed 20 times the most probable expectation is 10 heads and 10 tails, but frequent departures from this even result are to be expected. About once in 40 times a departure as large or larger than 15 heads or 15 tails is to be looked for. In the same way, many cattle raisers may expect to get 15 or more bull calves out of 20 births A deviating ratio of this kind obtained one year would have no effect whatever on the sex-ratio in the following year

Sex in plants.—Sex in plants serves the same purpose as

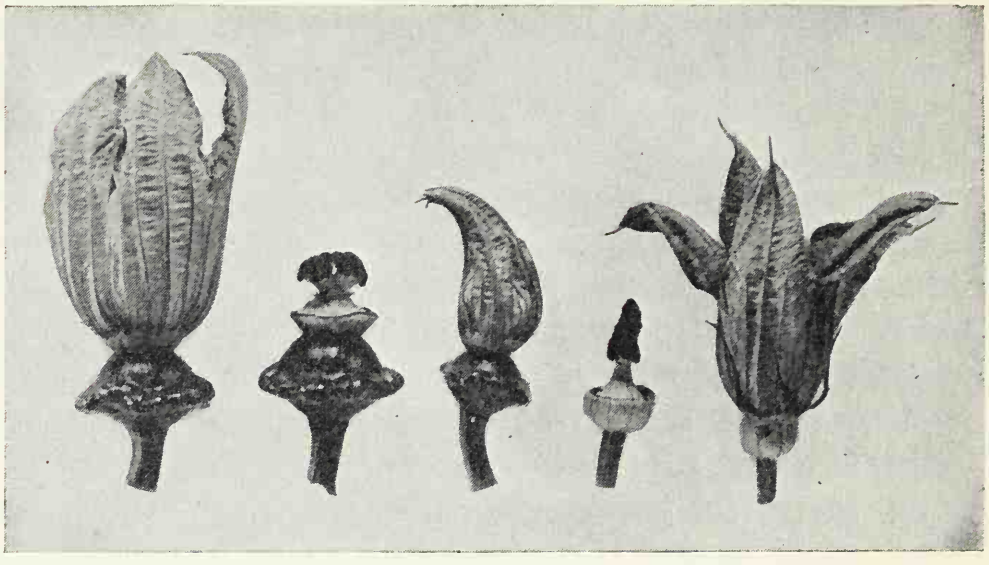


FIG. 63.—The two kinds of flowers borne on the same plant of squash (*Cucurbita pepo*). The seed-bearing or female flowers to the left; pollen-producing or male flowers to the right.

it does in animals. There are, however, important differences in this respect between the two kinds of living organisms. The higher plants are largely hermaphroditic and hence the pollen grains and ovules, as well as all of the tissue cells throughout the plant, carry the potentialities for both sex organs. Perfectly normal individuals of many species can be reproduced vegetatively from practically every part of the plant. During development, the floral parts are laid down in specialized areas in the same way that roots, stems, and leaves are differentiated. This is particularly clear in

monoecious plants, such as maize and the cucurbits, where the two types of flowers are separated on the same plant. There is evidence from only one species that differences in number of chromosomes have anything to do with sex in the seed plants. Among certain lower forms, where the sexes are separated on different plants, chromosome differences are apparently associated in some cases with particular floral types. The dioecious seed plants, such as poplar trees, mulberry, date palm, hemp, spinach, and asparagus, are apparently potential hermaphrodites in which the floral parts of one or the other sex have been suppressed.

Practical importance of sex.—Sex in seed plants has very little importance for practical breeding, with the possible exception of the date palm, in which it is desirable to eliminate the non-producing staminate seedlings at as early a stage as possible. With these plants the situation is much the same as it is with poultry. Ordinarily it is not possible to distinguish between the sexes of chicks until some time after hatching. On many poultry farms, specializing in egg production, the males are not desired, whereas for other purposes they can be used to advantage. It is now possible to separate the sexes of poultry at hatching time, if desired, by the use of appropriate sex-linked color characters. Certain colors and patterns can be recognized in the down, and it is possible to make matings in such a way that all the males will be of one type and all the females of another. This method was first suggested by Punnett of England, and has been extensively investigated and advocated by Dunn at the Storrs, Connecticut, Station. The application of sex-linked inheritance in this way to poultry production is given in detail in Chapter XV.

CHAPTER VII

VARIATIONS, LARGE AND SMALL

HEREDITY is generally understood as the tendency of succeeding individuals to perpetuate the characteristics, properties, and traits of their ancestors. The study of evolution in nature and of the improvement of animals and plants for economic purposes has its first concern not with the tendency of like to produce like but with the possibility of like producing unlike, that is, variation. We are familiar with the differences everywhere about us in the many varieties of cultivated plants and domestic animals. From the fossils preserved in the rocks, we know that forms once lived which differed from similar organisms now familiar to us. Variations which are inherited have occurred and are occurring. How frequently do these changes take place and under what circumstances? Which of them are persistent and which are transitory? Can permanent variations be produced at will, directed, or even predicted? To what extent can undesirable variations be controlled, modified or prevented? Many of these questions can not as yet be satisfactorily answered.

The hereditary factor has so far been considered as a stable unit which does not vary. If this is universally true, one is led to ask, "How do the alterations from which new forms come arise? Are all hereditary differences due solely to diverse associations of unchanging entities?" It is difficult to conceive of the great complexity of plant and animal life as due simply to environmental differences and to recombination of fixed determiners. However, there is evidence that factors do change. The horticultural literature is full of instances of the sudden appearance of radically

new forms both in seed and vegetatively reproduced plants. These striking changes have been called sports. They are now generally included in the term **mutations.** It is evident that many of the abrupt changes considered as sports by the early writers were merely Mendelian segregations. For example, if a white sweet pea were accidentally crossed with another white variety carrying a complementary factor for color, and the plants when grown the following year produced purple flowers, although the parent races had produced nothing but white flowers as long as known, such a striking appearance would doubtless have been called a sport. Many new forms are certainly due to segregation and recombination where the previous generations have been widely crossed.

Chromosome aberrations.—Variations which occur in different parts of the same plant, and which persist when these parts are used for vegetative propagation, have long been known and can not be due to ordinary Mendelian segregation, since this process occurs normally only at the reduction division preceding the formation of the sex cells. However much the reproductive cells may differ in chromosome composition, the tissue cells of the plant or animal are assumed to be all alike in regard to the factors they contain. But in some cases it has been demonstrated that abnormal changes occur in cell division, such that the chromosomes are not divided equally. Instead of the two members of each chromosome pair separating at the reduction division, both members of one or more pairs may go to one daughter cell, leaving the other without any representative of this particular chromosome. These daughter cells, therefore, differ in composition, some having extra chromosomes and others lacking them. The individuals produced from these abnormal gametes differ more or less strikingly from the normal type.

Heritable variations arising in this way have been found in many organisms and have been extensively studied by Blakeslee, Belling, and Farnham at the Carnegie Institution

at Cold Spring Harbor, Long Island, in the Jimson Weed (*Datura*). Differences in foliage, habit of growth, size and shape of seed pods, and character of the spines on the pods have been regularly associated with doubling in particular chromosomes. There are 12 chromosomes in *Datura* and many of these pairs when increased by the addition of one

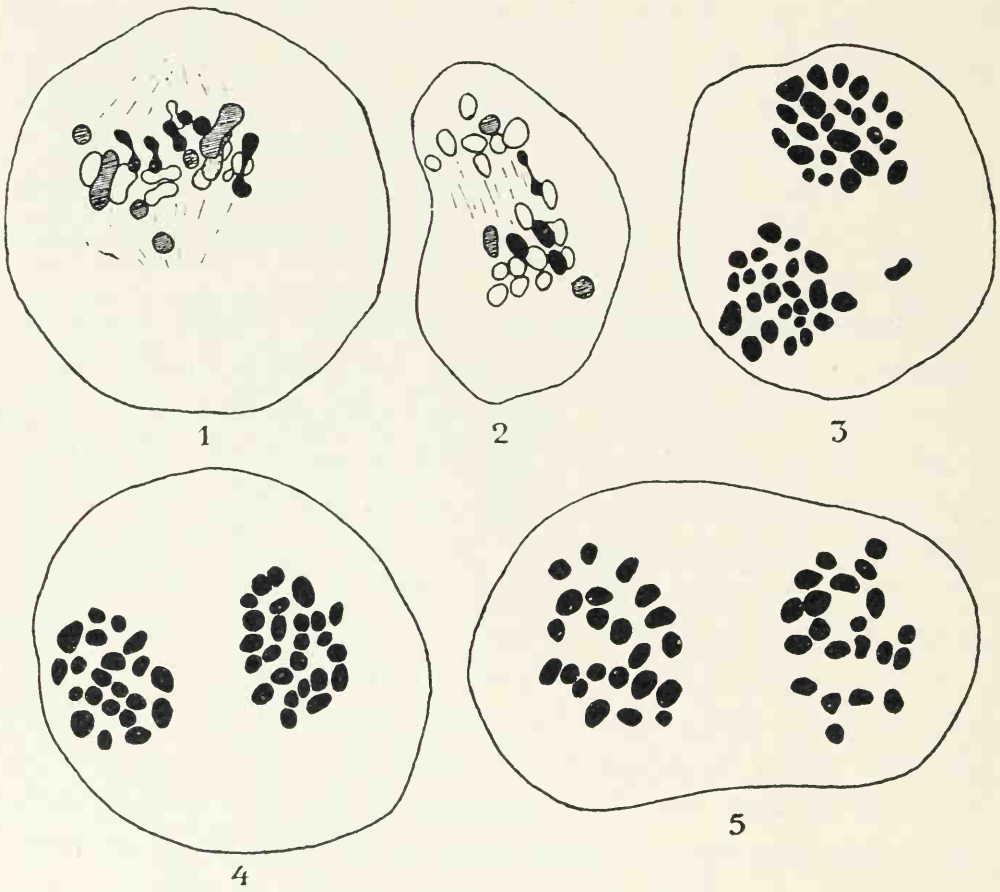


FIG. 64.—Unequal division of chromosomes in *Viola*, giving cells with unequal numbers of chromosomes. (After J. Clausen in Hereditas.)

more of its own members has produced a characteristic variation in the plant, and this is transmitted to all the offspring that receive the extra chromosome. Some of these variations are shown in Fig. 65. Many other combinations of chromosomes are possible, such as a doubling of several or all of the 12 pairs or the addition or subtraction of one or more chromosomes in individual pairs, as shown in Fig. 66.

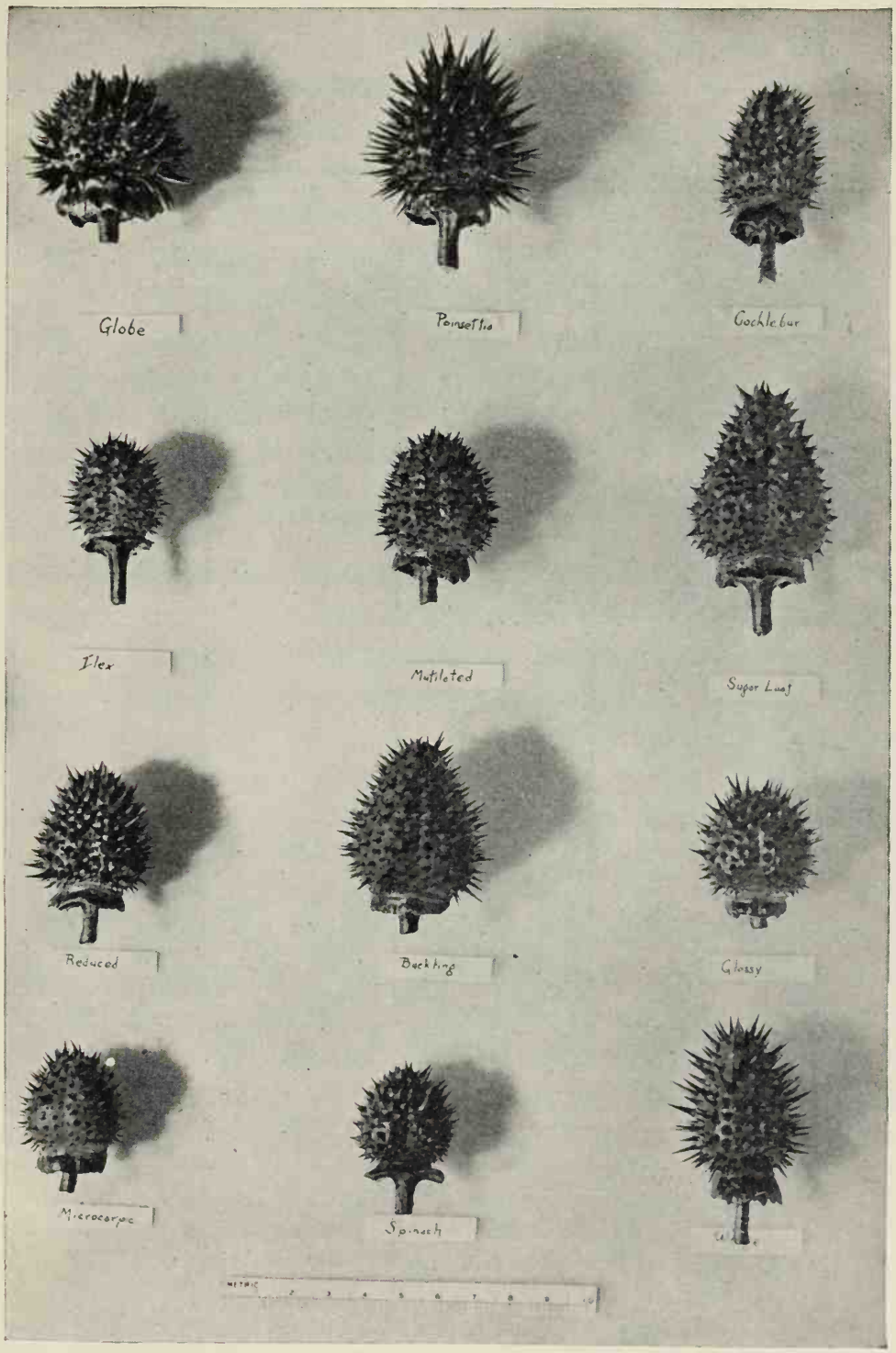


FIG. 65.—Variations in capsule form in *Datura* associated with abnormal numbers of chromosomes. (After Blakeslee in American Naturalist.)

Some of these groupings have been identified with clear-cut heritable differences in the plants.

It is now evident that rearrangement of tne chromo-

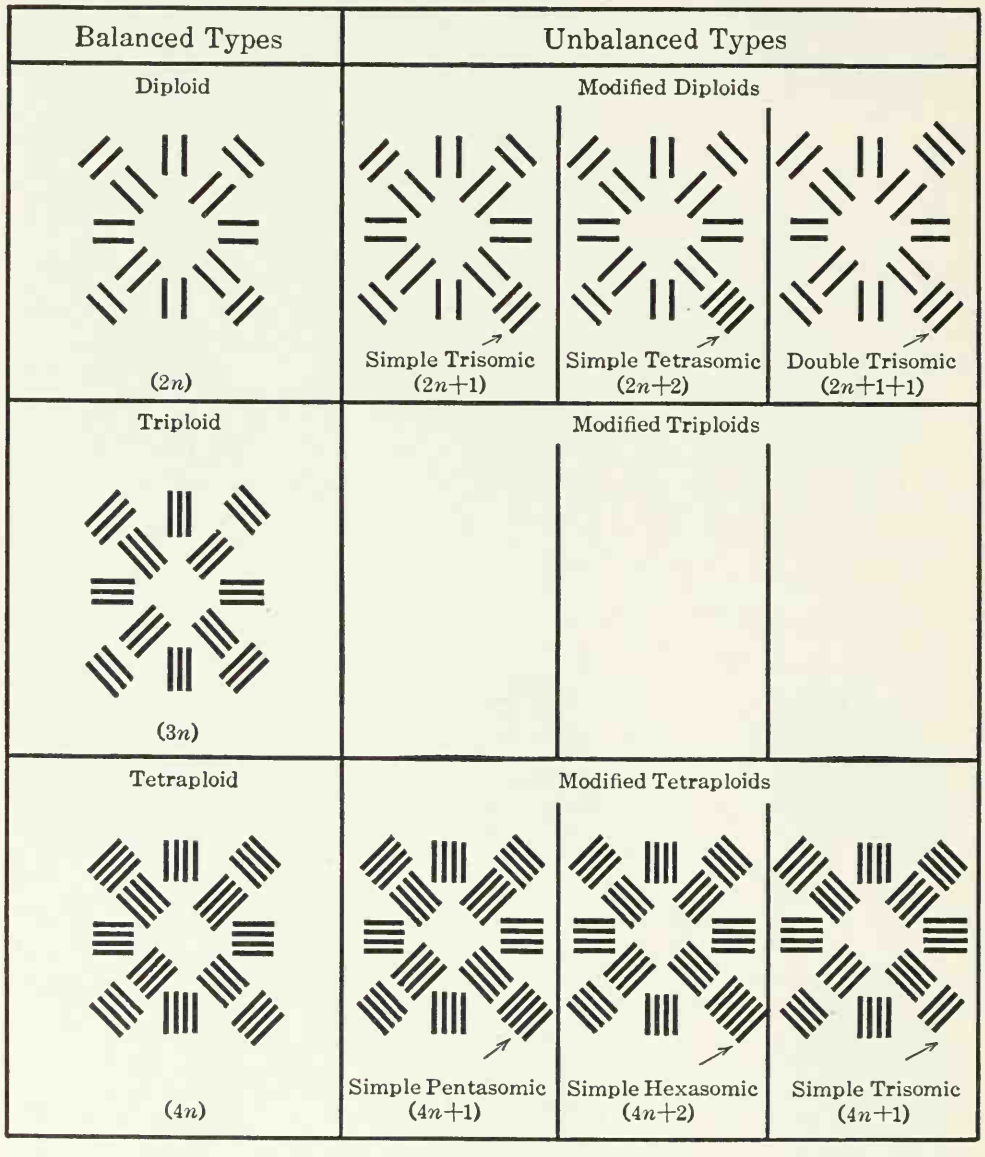


FIG. 66.—Diagram illustrating some of the chromosome combinations identified in *Datura* as being associated with characteristic changes in form. (After Blakeslee in American Naturalist.)

somes is a frequent cause of variations in many organisms. Since many related forms differ in chromosome number by multiples of some common number, it is probable that doubling of the chromosomes has been a factor in their

separation. This is well illustrated in wheat. Sax has found that common wheat has 21 chromosome pairs; several related species, such as emmer, durum wheat, Polish wheat, and Poulard wheat, have 14 pairs; while einkorn, which will not give fertile hybrids with any of the other groups, has 7 pairs. From a cross of two species of violets, one having 13, the other 17 pairs of chromosomes, J. Clausen has obtained a plant with a total number of 46 chromosomes, equivalent to 23 pairs. This is thought to be due to the failure of many of the chromosomes to pair and the subsequent division of the unpaired chromosomes. This indicates that plants with new chromosome numbers can arise from crosses of species which differ in this respect and that possibly these new chromosome types may come to form distinct species.

Changes in the Mendelian units.—In addition to these distinct variations, which originate in chromosome aberrations, similar abrupt departures are found where there is no reason to expect that a loss or reduplication of chromosomes has occurred. It is evident that some change has taken place in some one or more of the single determiners located in the chromosomes. Such variations are fully formed from the start, and it is to such changes as these that the term mutation is generally applied. They come forth in one generation, and when produced are relatively stable. When individuals possessing such a mutation are crossed back to the stock from which they arose, they usually show clear-cut Mendelian segregation in the monohybrid ratio. Variations of this kind, which are sufficiently large to be easily recognized, are rare. When they occur in uniform races in conspicuous parts of the plant, as, for example, a change in a flower from colored to white, from self-colored to striped, or in leaves from simple to compound or the reverse, and from the possession of horns to hornlessness in cattle, such departures from type attract attention immediately. They may arise only once in thousands of individuals; yet when they do, they may be easily noted. Other mutations

occur in minor or inconspicuous features and for the most part escape detection. Therefore, a mutation is not to be judged by its size or conspicuousness. Moreover, a single

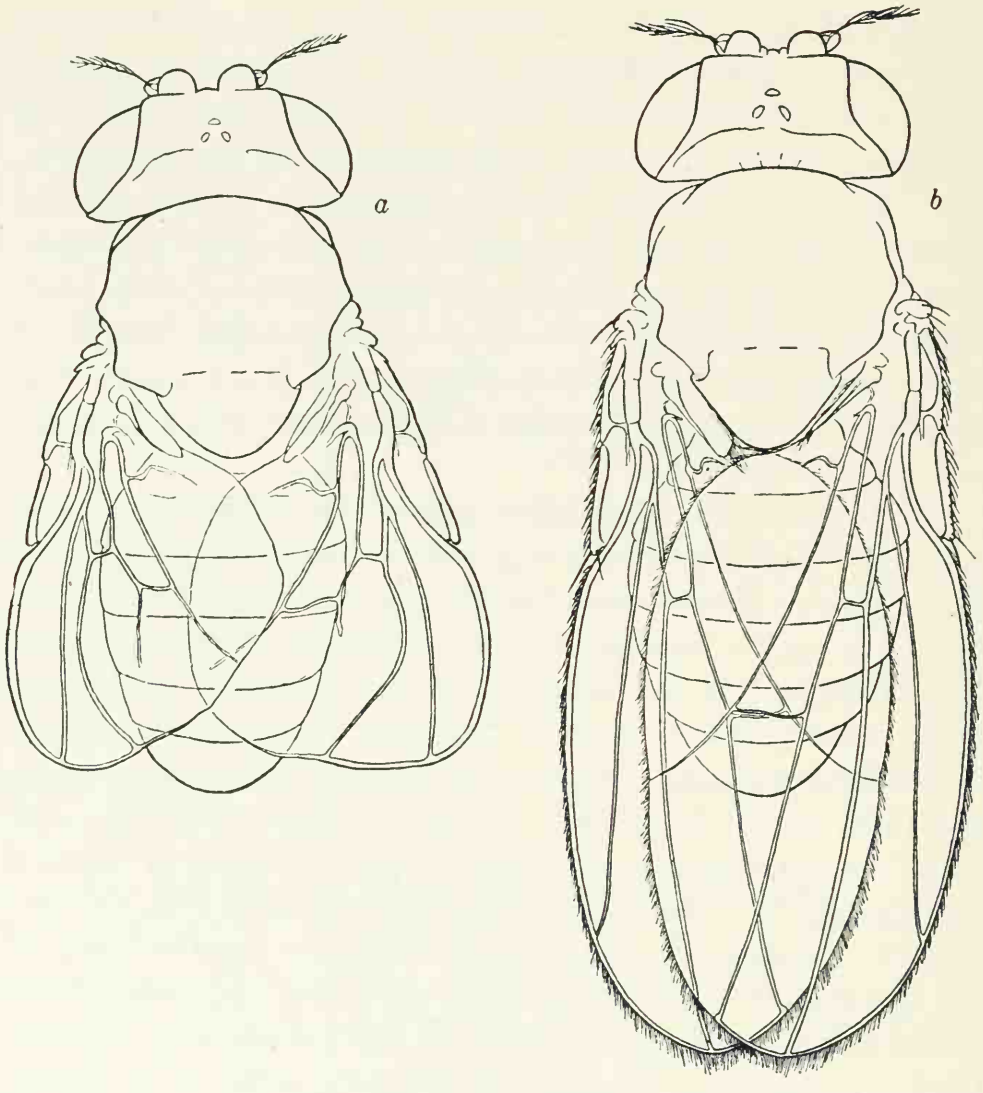


FIG. 67.—A mutation from normal wing (right) of *Drosophila melanogaster* to rudimentary wing (left), due to a change in a single gene. (After Morgan and Bridges in Carnegie Institution Publication No. 237.)

unit change may have profound effects on many parts of the organism.

Classification of variations.—Having in mind the modifying influence of the environment, the spontaneous mutations which occur in the hereditary factors themselves, and the

way that these factors and the chromosomes which carry them can be recombined, Baur has classified all variations in animals and plants in three general groups, according to the way in which they occur, as:

1. *Modifications*
2. *Combinations*
3. *Mutations*

Modifications are differences exhibited by individuals as a result of the unequal influence of different environmental conditions. Variations of this sort usually differ in degree rather than in type, and with large enough numbers the deviating individuals can be arranged in a graded series such that the change from one to the other is almost imperceptible.

Combinations are differences between individuals of common ancestry, caused by diverse associations of germplasm. There are two classes of combinations. The first and most common include the normal segregation and recombination of genes which take place during the reduction division at the formation of the germ cells, interchange of parts of chromosomes in crossing-over, and sexual fusion of gametes. The second class includes various forms of abnormal chromosome arrangement whereby the usual number of chromosomes is replaced by reduplicated or missing members. The former can be considered as gene combinations, the latter as chromosome combinations. Gene combinations have been illustrated in the examples of Mendelian heredity already given. Variations due to combinations may be either abrupt, clear-cut differences or they may fall into a continuous intergrading series and be quite similar to modifications.

Mutations are differences due to chemical or physical changes in one or more genes. In their effect they may be of large or small degree, but they occur so infrequently that intergrading series of forms which can not be clearly distinguished are comparatively rare.

Heritability of variations.—The first class of variations are not inherited; the other two are. This is due to the fact that the changes in the first class are only in the somatoplasm, while in the second and third classes they have their basis in the germplasm. With regard to their heritability, variations are therefore either **somatic** or **germinal.**

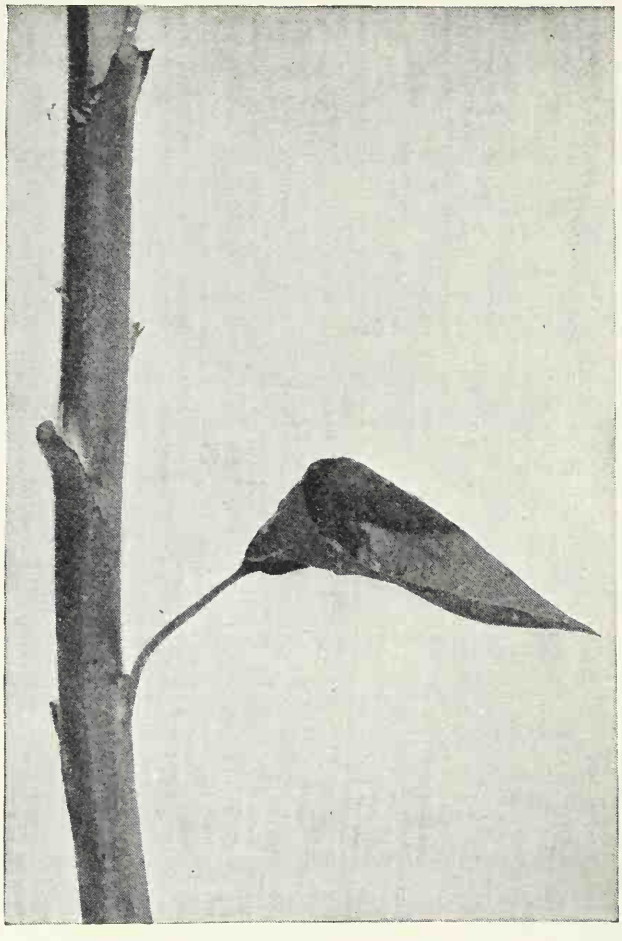


FIG. 68.—A cup-shaped leaf of tobacco, which is rarely found and not transmitted to the following generations. An illustration of a somatic variation during development, due to an unknown cause, which is not heritable.

Determining the cause of variations.—The three kinds of variations can rarely be distinguished by appearances. Their causes can only be positively known by the breeding behavior of the individuals possessing them. In the first category, *modifications*, the differences between individuals

are due to external causes arising from the many differences in the environment in which the organism and its immediate ancestors have developed. As shown in Chapter II, the surroundings and the treatment given to animals and plants have a profound effect upon them, and are an ever-present cause of variation and, as such, a matter of great concern in the business of plant and animal production. Although some changes induced by the environment may carry over from one generation to another, they are temporary and for this reason have no permanent value for plant and animal improvement by breeding. *Mutations*, on the other hand, owe their origin to inward causes and constitute a means by which organic life can be molded. As far as can be judged at present, there is no causal connection between these internal germinal changes and the external surroundings in which the organism develops. The variations are largely fortuitous in their appearance. At least, no satisfactory means of producing mutations at will have yet been discovered. They are the material, however, with which Mendelian *combinations* are made, and this last type of variation is practically inexhaustible. Given races of animals and plants with diverse characters, recombination of the units of inheritance which they already possess makes possible an endless complexity of forms from which to choose. Since combinations of factors can be induced by crossing as desired, this is the type of variation which offers the greatest opportunity for improvement. Even though reassortment of comparatively permanent Mendelian factors is chiefly responsible for the diversity of domesticated species, mutations are not without value. For practical purposes it is not necessary to distinguish between the two kinds of heritable variations, since both are transmitted from one generation to the next.

The nature of variations.—Without relation to their cause, variations are classified as to their *nature* according to their effect upon **structure** and **function.**

Structural variations result from differences in size and

form. They may be due to repetition in the number of parts, such as nodes and internodes in the stalk, petals in the flower, leaflets in a compound leaf in plants, and phalanges in animals; or they may be due to the replacement of one part by another or to alteration in the form of the individual parts. Differences in quality result from variation in physical and chemical composition. Thus the texture of tissues depends upon the thickness of the cell walls and the physical construction of the various parts. Resistance to drought, disease, cold, or injurious substances in the soil, such as alkali, varies according to the physical and chemical composition of the individual and race.

Functional variations result from differences in performances, such as ability to grow and to produce accessory parts, including milk, eggs, wool, fur, etc. Differences in speed, strength, and endurance in draft animals are functional variations closely dependent upon structural differences. Variation in mental capacity falls largely within the field of eugenics, although differences in this respect merit the attention of livestock breeders.

It should be noted that this classification is purely an arbitrary one, made for convenience. Structure and function are so closely interdependent that it is not possible, and seldom necessary, to make any real distinction between the two.

Variations classified as to type.—According to *type*, variations may be distinguished as **continuous** and **discontinuous.** Continuous, or fluctuating, variations may be due either to modifications from the environment or to different combinations of hereditary factors. Both are usually concerned. Such variations may also result from mutations. Very small changes are sometimes inherited. Intergrading variations are usually met with in size characters, although differences in form and color are sometimes so small as to make separation impossible. Abrupt variations are more common in form and color, such as the change from single to rose comb in fowls, simple to compound leaves

in plants, and from one distinct color to another in all forms of life. Clear-cut differences in size also are found, as in the production of dwarf forms in both animals and plants. Discontinuous variations are largely due to differences in germinal construction resulting from different combinations of hereditary factors or mutations in the factors themselves.

The direction of variations.—In regard to their *direction*, variations are said to be **fortuitous** or **purposeful.** Usually, variations occur in all directions as if they were due entirely

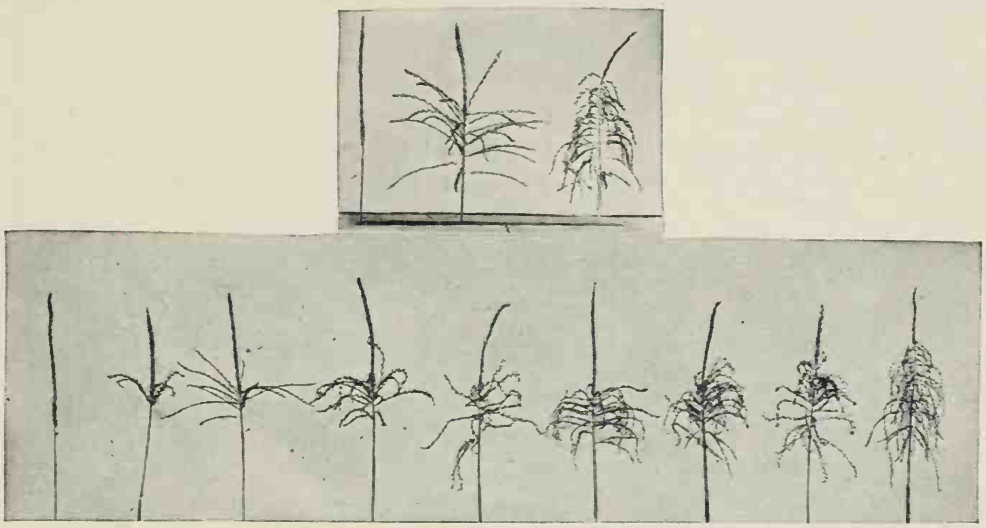


FIG. 69.—The result of crossing a variety of corn having unbranched tassels with a profusely branched variety. The parents and F_1 above, F_2 below. An illustration of continuous variation due to different combinations of hereditary units.

to chance. However, the geological records show that changes in certain parts, occurring during long periods of time, have tended in certain definite directions. Whether the variations actually occur more frequently in one direction than another, or whether natural selection has preserved more of one kind than another, is disputed. There are examples among living forms, however, which seem to indicate variation along a certain line. The ostrich is tending towards a reduction in the amount of feathering and in the number of toes on the feet. In ferns, there is a definite tendency to increase the complexity of the compound leaves.

Finally, as to *origin*, variations are either **external,** differences which have their basis in conditions acting upon the organism from without, or **internal,** differences resulting from the interaction between the germplasm and the somatoplasm.

How modifications are brought about.—The external causes of variation are numerous and obvious. They are all

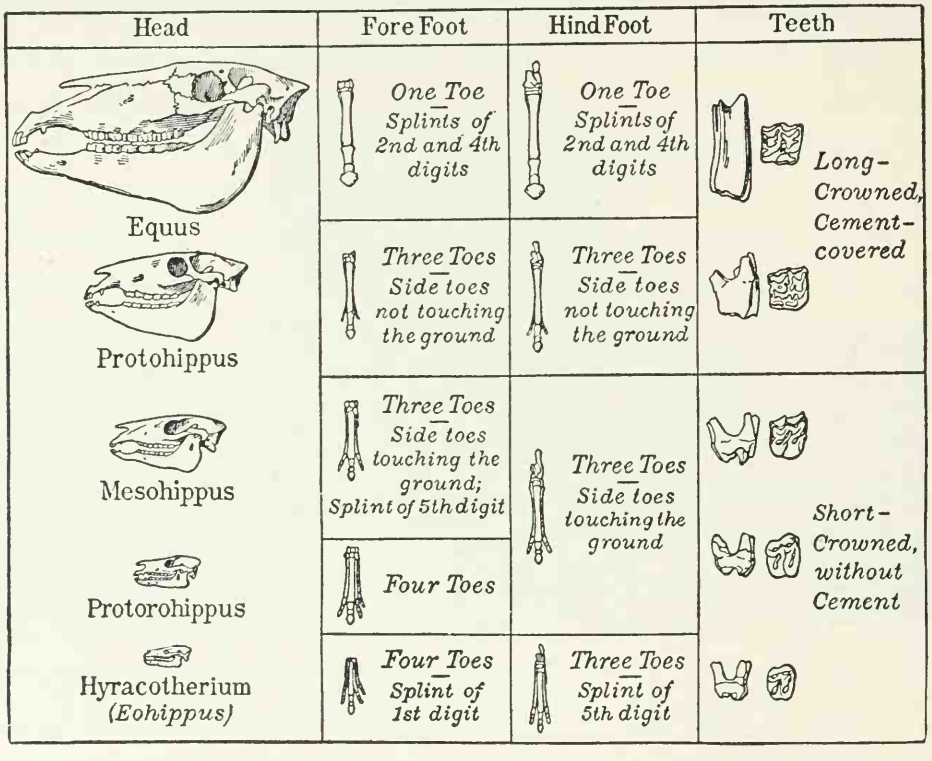


FIG. 70.—A series arranged from fossil and recent remains of the horse and his assumed ancestors, showing a continuous change in a definite direction. (After Osborn in "Origin and History of the Horse." Proceedings of the New York Farmers.)

included in environment and training. The principal effects of the environment come under the headings of food, light, temperature, moisture, and parasitism.

Food.—Differences in food have a pronounced effect on all forms of life. Not only the amount of food but the kind of food is important. Osborne and Mendel, at the Connecticut Station, have kept rats alive, but without growth, by feeding all the animals would eat of a ration deficient in

certain proteins. Malformation of the eye and other pathological conditions are the direct result of improper

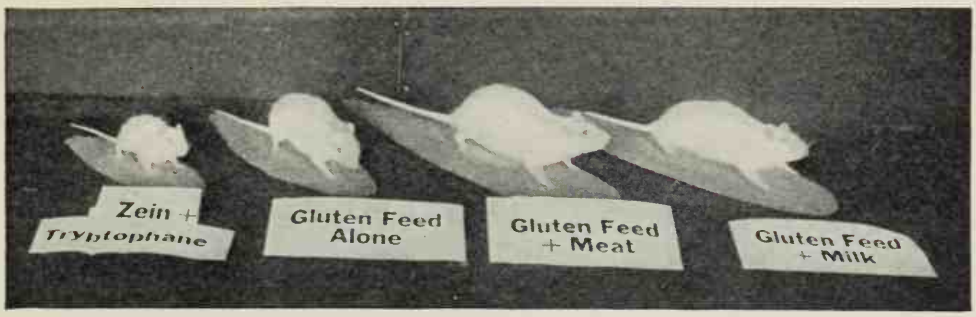


FIG. 71.—The effect of the kind of food upon growth. These rats are all of the same age and were fed for the same length of time on diets containing the same proportion of protein from corn and other substances. The variation in size is due to differences in the chemical constitution of the proteins eaten. (After Osborne and Mendel.)

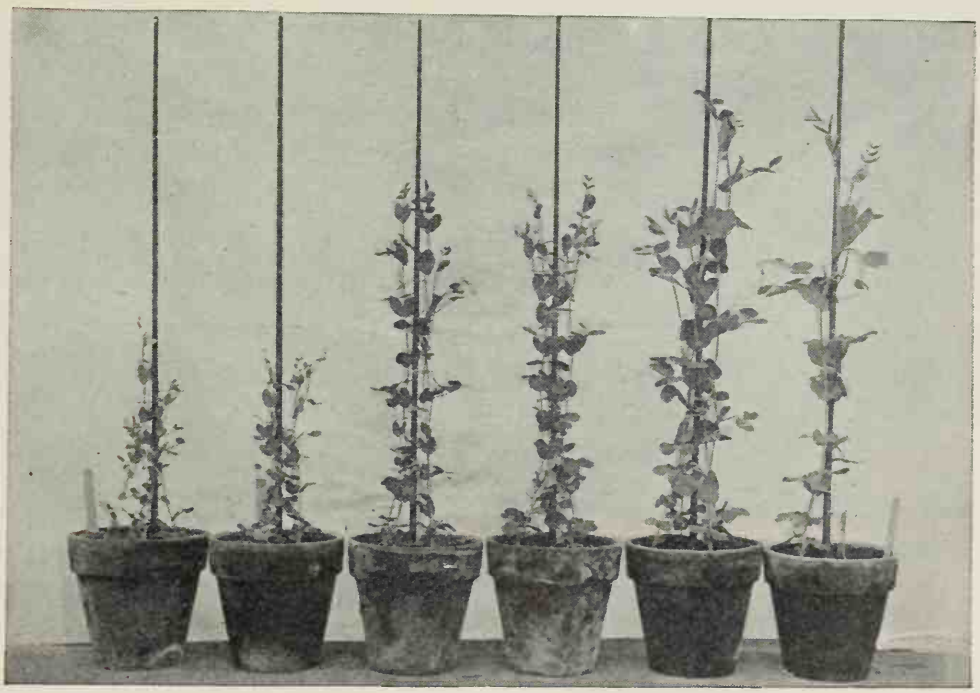


FIG. 72.—Variation due to differences in the fertility of the soil. Peas grown in sand, medium and well-manured soil, two pots of each type of soil. (After Love in Cornell A. E. S. Bull. 293.)

diet. Scurvy, pellagra, and beri-beri are some of the common diseases, to which man is subject, that are attributed in part at least to a lack of essential substances in the food.

Light.—The production of chlorophyll, the green coloring matter by means of which plants convert the carbon dioxide from the air and water from the soil into sugars and starches, is absolutely dependent upon light. In addition, certain other colors are modified by light. Certain kinds of corn produce a red color where they are exposed to sunlight at the

FIG. 73.—A variety of soy beans in which seed production and early maturity is favored by decreasing the length of the daily period of sunlight. (After Garner and Allard in Jour. of Agr. Research.)

tips and along the sides of the ears; if the husks are removed during the growing season the ears are uniformly colored throughout, but when completely covered so as to exclude light they are colorless. Other kinds of corn are colored whether exposed to light or not. The factors which make possible both kinds of color are inherited, but one is modified while the other is not.

The amount of light and the relative duration of daylight and darkness have a profound effect upon growth and reproduction in plants, as shown by Garner and Allard of the United States Department of Agriculture. The period of sunlight varies with the season and geographical position. Plants have become adapted to different relative periods of light and darkness for their proper functioning. Shorten-

FIG. 74.—Red Clover is prevented from flowering by shortening the exposure to sunlight. (After Garner and Allard in Yearbook of the U. S. Dept. Agr. for 1920.)

ing or lengthening the period of light causes many plants to stop vegetative growth, and to flower and set seed. Many varieties of soy beans, when grown in the North, make a rank growth of stems and leaves but produce few flowers and these so late as to ripen few seeds. When the plants are kept in darkness and exposed to daylight during about half the usual day, they flower early and produce a heavy crop of seed. The plants grow to about half their usual size.

On the other hand, clover in reduced light retains a prostrate habit characteristic of its growth in the fall, and does not flower. The radish, which normally sends up a flower stalk in midsummer, sets seed, and dies, will produce only leaves if the daylight period is artificially shortened. The early planting of certain vegetable crops, such as peas and spinach, is necessary in order to adjust the plants to their optimum light requirements.

Temperature.—The coloration in some plants and animals is altered by changes in temperature. In the Arctic regions, many species of animals change color with the seasons, being a gray or neutral color in the summer and white when the snow is on the ground. Insects reared at different temperatures differ in color and markings. The peacock butterfly, *Vanessa io*, when subjected to unusual temperatures by Goldschmidt, produced a series of forms in which the " peacock eye " mark was gradually faded out.

If plants of a red variety of the Chinese primrose (*Primula sinensis rubra*) are exposed to a temperature from 30° to 35° C. for about one week before blooming, they will produce pure white flowers. If some entirely similar plants of the same variety are exposed, for the same period, to a temperature from 15° to 20° C., the flowers when they appear will be red. Thus, as Baur, who performed this experiment, states, it can not be said that this *Primula* inherits either red or white flowers. What is transmitted from one generation to the next is the ability to react in a certain way to the temperature in which it is grown.

An eyeless Drosophila, which shows its typical form only when reared at a fairly high temperature, is reported by Hyde. At low temperatures the flies are entirely normal. Moisture also has a controlling influence, as the number of individuals with reduced or missing eyes increases as the culture medium becomes drier.

Moisture.—An illustration is furnished by Drosophila, as described by Morgan, in which an abnormality is produced under conditions of high humidity. The normal

black bands on the abdomen in certain families are broken and irregular, or even entirely missing, when these flies are raised on moist food. As the culture medium becomes drier and less abundant, the flies that emerge are less abnormal, until finally individuals appear which do not seem to differ from normal flies. If food is plentiful and kept moist, this change does not occur; and if the food is kept dry from the first, all the flies are normal.

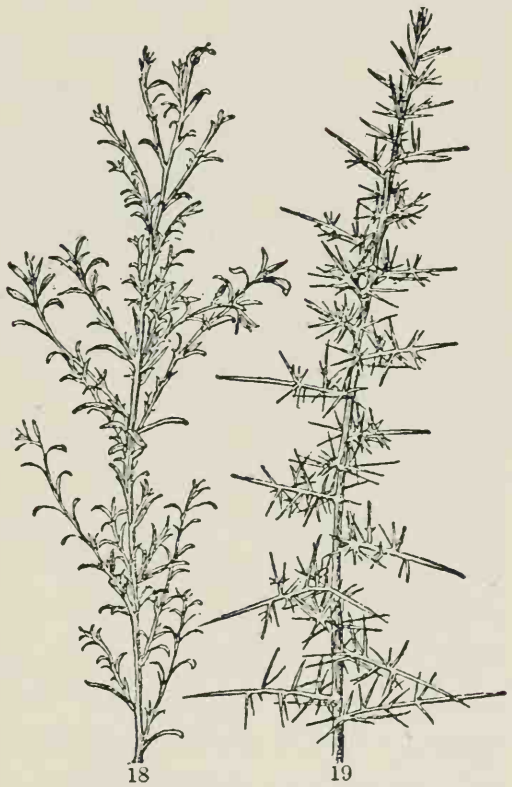


FIG. 75.—Two plants of gorse (*Ulex*), showing the effects of differences in moisture. The plant on the left was grown under moist conditions, the one on the right under dry conditions, the leaves and branches having developed as thorns. (After Lothelier from Coulter in "Fundamentals of Plant Breeding," courtesy of D. Appleton & Co.)

Parasitism and symbiosis.—The parasitic and symbiotic relations among different animals and among different plants are numerous and varied. An illustration of extreme change in structure in plants is furnished by the numerous gall-forming insects which work on many plants. Other marked changes are produced by such fungous diseases as ergot in rye, smut in corn, black knot on plums, and club root on cabbage. Variegation in the color of foliage of many plants is caused by an infectious disease of some sort, such as mosaic in tobacco, tomatoes, and potatoes, and chlorosis (disappearance of the chlorophyll) in roses and other plants. Pathological conditions are equally common in animals and often profoundly alter their size, form, and rate of growth. Resistance to disease has its basis in

heredity in many cases, but the actual infection comes under the heading of environmental causes of variation.

Organisms that are mutually helpful are illustrated by legumes and the nitrogen-gathering bacteria that inhabit their roots. The fungi growing upon roots of certain pines, beech trees, and blueberries and their relatives have an important symbiotic relation with their hosts, and the growth of the plants is largely dependent upon the extraction of food from the soil by these organisms.

Variations having internal origin.—Spontaneous changes which occur in certain parts of a plant and persist in later generations, whether grown from seed or propagated by vegetative means, are spoken of as bud mutations. A change which takes place in a single cell is usually not noticeable until sufficient tissue has been formed from it to make a bud from which a branch is produced. If the bud is formed wholly from the new tissue, the branch may differ strikingly from the main plant, as shown in Fig. 76. A gladiolus plant with white flowers may have colored flowers on the same stalk. Peach trees have been known to produce fruit entirely free from pubescence. When buds for propagating are taken from such a branch, a new type of peach characterized by smooth-skinned fruit is obtained. Such is the origin of the nectarine. This new fruit may remain constant for the glabrous condition of the epidermis for long periods of time in asexual reproduction, and then for some unaccountable reason it may change back to the fuzzy fruit of the peach. But when the nectarine type of fruit is once produced, all varieties of peaches can be changed over into nectarines by crossing with such a form.

Carrière, an early French writer on plant improvement, mentions a number of vegetative sports, of which the most striking are white flowers produced on a red rose and a red-flowering branch on a yellow rose bush. Cramer lists over four hundred named varieties of chrysanthemums which have originated in this way.

Sugar cane having only green stalks has been known to

give pure-colored and striped stalks, which have been the basis for the establishment of new varieties. Such new

FIG. 76.—Variation in color and shape of leaf in *Euonymous*, due to a transmissible alteration in a particular part of the plant. (After Shamel in Jour. Heredity.)

forms may differ in sugar content and productiveness as well as in the more noticeable color characters. Potatoes

have been extensively investigated, and a small number of permanent variations in tuber lines have been found. Characteristic oblong potatoes have changed to round forms, which continue to reproduce the new shape. Tubers with shallow eyes have given deep eyes, and colored varieties have given white-skinned potatoes. These changes have been found only after examining many thousands of plants. Many variations of the same kind and degree have been found but have not persisted in the plants grown from the deviating plants. Instead, the progeny go back to the

FIG. 77.—Deep-eyed variation in the potato at the right was found to persist in vegetative propagation. (After East in Conn. A. E. S. report, 1909, 1910.)

original type, showing that these variations did not take place in the tissues which are used in reproduction but are due in some way to the surroundings and not to any germinal change.

Difficulty of distinguishing between factor mutations and abnormal chromosome distribution.—In the foregoing illustrations of bud mutations, there is no certain way of knowing at the present time whether the mutations are due to actual changes in the nature of the genes themselves or to irregular distribution of chromosomes during cell division in growing tissues. In heterozygous individuals, the removal of the chromosome containing the dominant allelo-

morph, due to its failure to divide and separate normally, leaves the recessive factor free to show up. Presumably a change from a recessive to a dominant character is an indication of a factor change rather than irregular chromo-

FIG. 78.—Tobacco plants which do not flower under normal conditions. A conspicuous variation from the usual type in a naturally self-fertilized plant, which has persisted in plants grown from seed produced by growing the plants in a shortened day. (After Hayes in Jour. Heredity.)

some distribution, but unless a careful factor analysis is made one can not be sure which are dominant and which are recessive characters in any particular material. Moreover, from Blakeslee's results with *Datura* it is evident that

chromosome reduplication is a frequent cause of new variations, which may easily be taken for dominant factor mutations since they persist in plants reproduced by seed as well as vegetatively.

Mutations in sexually reproduced organisms.—Similar changes occur in organisms reproduced sexually. Plants which are naturally almost continuously self-fertilized, and for that reason are very uniform and constant, sometimes

FIG. 79.—The non-flowering mutation in tobacco (center) compared with the variety (left) from which it originated and the F_1 cross (right) between these two forms.

produce quite unusual forms. A good illustration is found in tobacco. This plant is generally self-pollinated. In a field of tobacco grown in Connecticut, among many millions of plants, a few were found at the end of the season which had produced no flowers and were taller than the plants which had flowered. Tobacco is usually very prolific in flowers and seeds. The general habit of growth is a straight stem with from 15 to 25 leaves and having branches at the top in a large inflorescence. The unusual plants produced

no branches whatever. Instead of the common number, they had more than 50 leaves. One of these plants was dug up and transplanted to the greenhouse, and later it flowered and made seed. This was sown the following year, and all the plants reproduced the mutant habit of growth, no flowers being formed in the open field. The plants grew luxuriantly, having more than 100 leaves, and at the end of the season were much taller than ordinary tobacco plants. The striking difference in habit of growth makes this new form easy to recognize. The fact that it has been found to occur only a few times in many millions of plants seems to preclude the possibility that such changes are due to Mendelian segregation. As the plants flower during the winter when the period of daylight is shortened, this type of tobacco can be reproduced by seed. Because the extra production of leaves makes it desirable as a commercial variety, it has been tested on an extensive scale. It has always persisted in the indeterminate type of growth. The shape and other qualities of the leaf have not been greatly altered, although the leaves are somewhat thinner and lighter in color, probably because they are produced in much larger numbers.

Breeding behavior of mutations.—When this mutant tobacco is crossed with the normal type, the determinate habit of growth is dominant, and the non-flowering, many-leaved plants are segregated out in the following generation in a simple monohybrid ratio. The change apparently has taken place in a single factor. Such changes usually occur in only one of the two allelomorphs. Whenever the mutant gene is recessive to its normal mate, the mutating individual does not show any change unless the mutation occurs in the dominant member of a heterozygous pair of factors. Ordinarily, recessive mutations are visible only in later generations, when, by matings between heterozygous individuals, the new form appears. Therefore, when mutations are seen, there are usually more than one of the same kind of deviating individuals and they breed true from the start.

For the same reason, mutations are more frequently seen in hybrids.

Chimeras.—In grafted plants it is, of course, necessary to distinguish carefully between actual bud mutations and branches which grow from the stock below the union. Sometimes it happens that a bud forms right at the junction of stock and cion, so that tissues of both are included in the branch that grows from this compound bud. In this way, by vegetative propagation, it is possible to produce an

FIG. 80.—The F_2 generation from the cross of the indeterminate, non-flowering variety with the original type, showing inheritance of this character as a simple Mendelian recessive.

entire plant, and from that a variety, made up of a mixture of two separate kinds of tissue which remain distinct. These combination plants are called graft-hybrids and are included in the general class of variations known as **chimeras.**

Graft-hybrids have been produced experimentally. Winkler grafted the tomato on the nightshade and the reverse. After they had united, the cion was cut off by passing the knife through the place of union as shown in the diagram in Fig. 81. The adventitious buds that were formed on the border line between the two kinds of tissue were

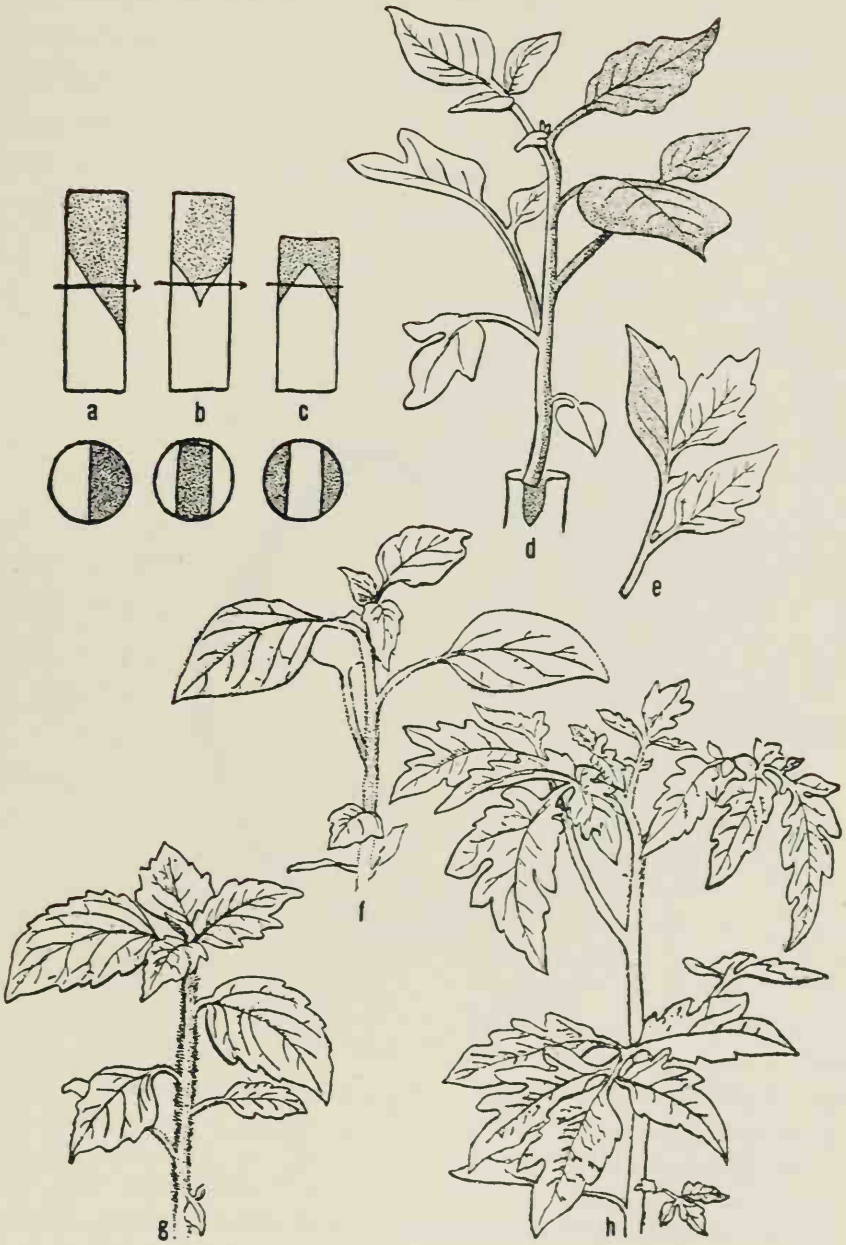


FIG. 81.—Diagrams showing methods used by Winkler in producing the tomato-nightshade chimeras, and some of the results. The shaded portions represent cion tissue; unshaded, stock tissue; *a*, *b*, *c*, various forms of grafts made; *d*, sectorial chimera (shaded portion, nightshade; unshaded, portion, tomato tissue); *e*, chimera leaf, part nightshade, part tomato; *f*, nightshade; *g*, perclinal chimera (nightshade body with tomato epidermis); *h*, tomato. (After Winkler from Babcock and Clausen in Genetics in Rel. to Agr.)

allowed to grow. From these, branches were formed which were part nightshade and part tomato. The characteristic growth of each species was exhibited separately in different parts of the branch. Other branches and plants propagated from them were uniform throughout and were unlike either parent. By examination it was found that in the

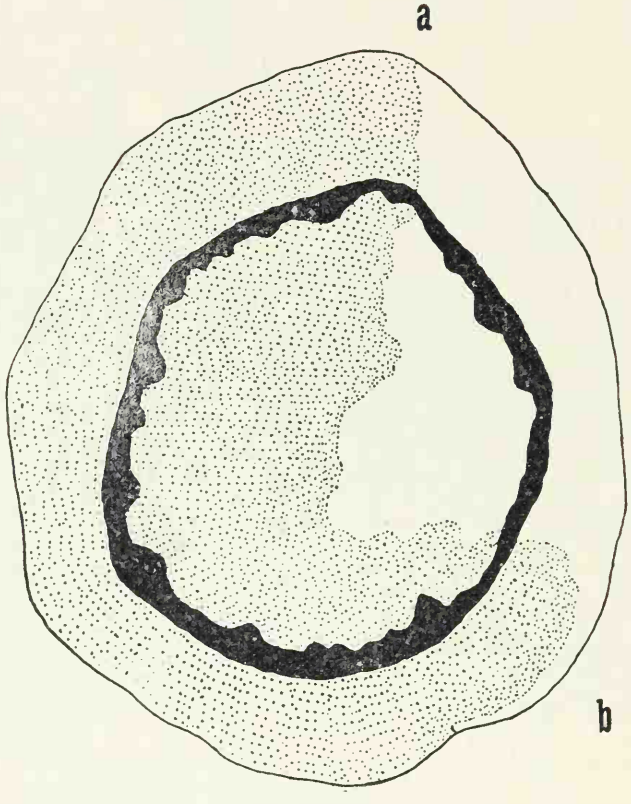


FIG. 82.—Cross-section of a stem of a sectorial chimera formed from two kinds of tissue from two different types of plants. A bud pushing out at *a* would produce another sectorial chimera, whereas one forming at *b* would give a periclinal chimera. (After Baur in "Einführung in die Experimentelle Vererbungslehre," courtesy of Gebrüder Borntraeger.)

former case the two kinds of tissue simply developed side by side. Such forms are called **sectorial chimeras.** In the other case the tissue of one sort was entirely enclosed by the other. Such forms are known as **periclinal chimeras.** The way in which these two types of graft-hybrids originate is illustrated in Figs. 82 and 83.

After making 268 grafts and examining more than 3000

shoots, Winkler found several distinct types which retained their peculiar form as long as propagated vegetatively. Some consisted of nightshade tissue within and layers of various thicknesses of tomato cells without; others consisted of the reverse combination. The form of the plants and the shape of the leaves differed markedly. The nightshade has 72 chromosomes and the tomato 24. By cytological examination, the two classes of tissue have been identified by their chromosome number and are known to remain distinct.

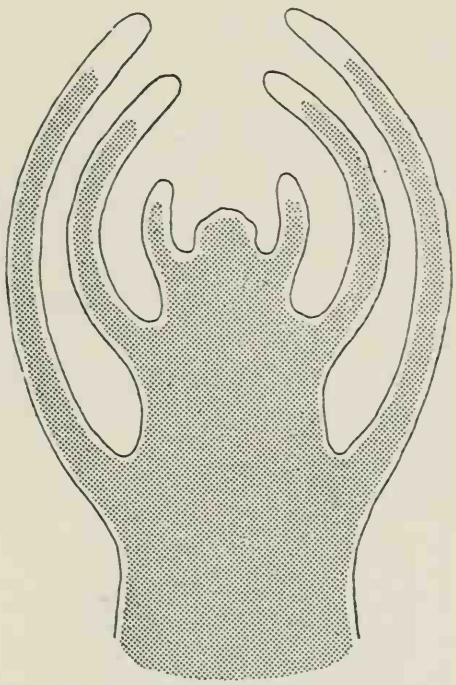


Fig. 83.—A diagram of a longitudinal section through a young shoot of a periclinal chimera, having one kind of tissue entirely within and another kind without. (After Baur in "Einführung in die Experimentelle Vererbungslehre," courtesy of Gebrüder Borntraeger.)

The fruits of these mixed plants closely resemble the form typical of the species that makes the internal part of the plant. The seeds from these fruits produce only pure tomato or pure nightshade plants. This is to be expected, since the germ cells arise from the sub-epidermal layers. Thus it appears that in such a graft-hybrid the two kinds of tissue retain their individuality, although the external form and features of the plant are greatly changed.

In 1826, a singular ornamental plant, known as Adam's Laburnam, originated from the Purple Broom (*Cytisis purpureus*) grafted upon the Shower of Gold (*Laburnam vulgare*). This is now known to be a periclinal chimera. Other combinations, including those of Whitethorn and Medlar, Quince and Pear, Almond and Peach, Tomato and Egg Plant, Tomato and Bittersweet, have been described.

Chimeras also result from mutation in the somatic cells

in the growing plant and may be perpetuated by vegetative propagation. Norton gives an illustration of a tomato which produced a branch having a lighter green foliage. The change apparently occurred in a single cell. The tissue from this cell, expanding as the plant grew, produced a variegated leaf. Later, an entire branch was formed of the lighter tissue. Striped oranges and lemons, differing in

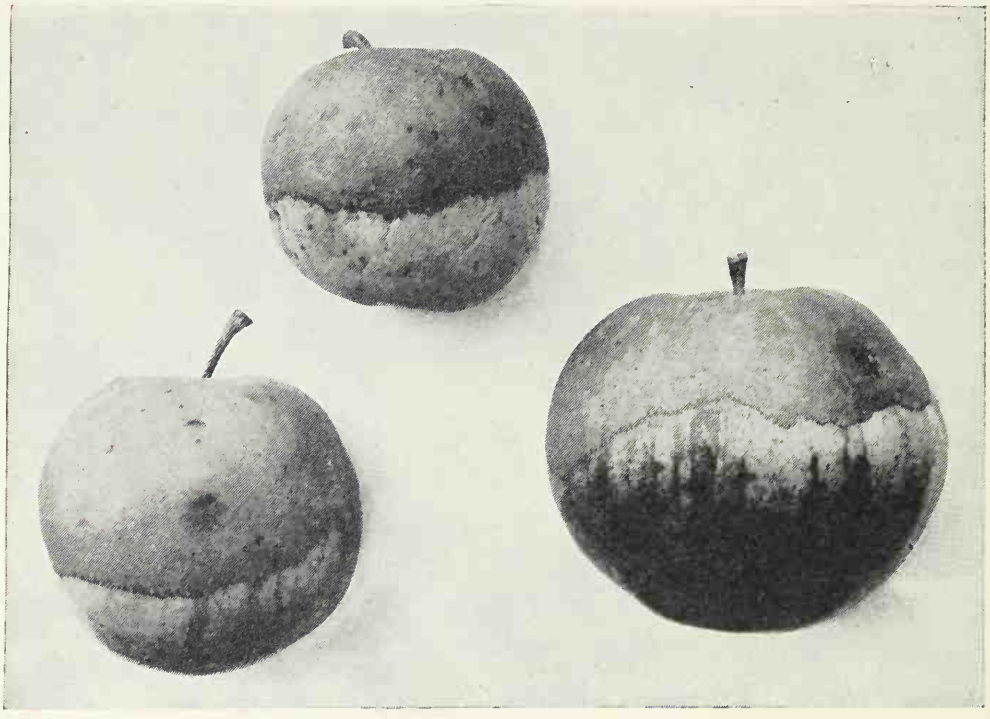


FIG. 84.—Sectorial chimera in the apple, in which part of the fruit is russet and part smooth skinned. The tree that produced these mixed fruits also produced unmixed fruits of both types. (After Castle in Jour. Heredity.)

color and texture of the rind, are produced in the same way by changes which occur, by some germinal alteration, in single cells, from which extensive areas of exposed tissue are later formed.

Germinal changes in the somatic tissues of the higher animals can not be easily identified and can not be proved directly on account of the impossibility of reproducing from the altered parts as in plants. Abrupt changes occur, how-

ever, in sexually reproduced individuals, animals as well as plants. These changes are due to permanent changes in the germ cells or in the tissues from which they are formed.

Mutations in animals.—Hornlessness in cattle is due to a mutation. Tailless breeds of cats have undoubtedly originated in the same way. The most authentic examples of mutation have been furnished by the experiments with the fruit fly. One of the first changes noted in this insect was the loss of red color in the compound eye. This structure in Drosophila is very conspicuous and any marked change in color naturally would be one of the first variations to be observed. One white-eyed male fly was found among several hundred individuals. The same mutation has occurred at other times, but only in very few individuals, considering the numbers observed. Similarly, the outline of the eye has been changed from nearly round to bar-shaped. Wings have become shortened and much reduced in size or nearly lost. The body color has changed from gray to yellow, to black, to sooty, and to ebony. While the total number of diversities which breed true in Drosophila is considerable, it must be kept in mind that they have been found only after a careful examination of millions of flies. No other animal or plant has been worked with in pedigree cultures in such immense numbers as Drosophila.

Such mutations as have been mentioned are considered to be due to some chemical change in a definite place on the chromosome. More than one change may occur in any one locus, making a series of factors, any two of which may form a contrasting pair and show simple Mendelian segregation, already described as multiple allelomorphs. The series of eye colors in Drosophila was not found, however, one step at a time. White eye originated directly from red eye, and the intermediate colors were found later, coming either from red-eyed flies or those with other colors.

The nature of mutations.—The principal feature of mutative changes is that they are discontinuous, abrupt dif-

ferences which appear fully formed from the start. It is the large, striking variations which are observed; the smaller departures from normal usually escape detection. For the most part, mutations are losses of certain characters and they are nearly always recessive. Of the more than 150 mutations in Drosophila, all but about 10 are recessive. Moreover, nearly all of the new characters are unfavorable to the development of the animals possessing them. Some of the mutations are so weakening that the flies possessing them are raised with much difficulty. It is seldom possible to have many recessive factors combined in one individual on account of the poor viability of such flies.

In the course of evolution, all variations which favor an organism in its growth and reproduction have been perpetuated. It is therefore a difficult matter to introduce any change which is an improvement. On the other hand, many variations may arise which are in the nature of retrogression and which tend to unfit the organism for development. In complex chemical substances such as the organic compounds which form the hereditary determiners, slight changes which have a profound visible effect may easily be conceived as occurring. In a living plant or animal, which is like a delicately balanced machine, any change is most likely to produce a result such that certain parts of the organism are unable to develop normally. Entirely new characters do arise, and variations occur which are decidedly more helpful to the organism, but they are found so rarely that mutations offer small hope of improvement.

The mutation theory.—A Dutch botanist, De Vries, first proposed the mutation theory to account for many diverse forms he found originating in the wild and in controlled cultures of many different species taken from the wild. The evening primrose was one plant which, more than any other, was seen to produce unusual offspring. The new types were found to occur so infrequently that De Vries thought they could not be due to Mendelian segregation. Some of the variations in the evening primrose found by

De Vries were undoubtedly due to actual germinal changes, such as are now understood as mutations. He also found many other examples of this type of variation in other plants and deserves great credit for calling the attention of the scientific world to this way in which new material is offered for natural selection to work on. However, many of the changes which De Vries at first considered to be mutations, he now considers to be due more probably to segregation from complex hybrids showing partial sterility and to chromosome aberrations. The evening primrose (*Oenothera Lamarckiana*), is not an established species. It has never been found growing wild to any extent and is considered to be a hybrid escaped from cultivation. Many of the seeds of this plant are aborted, and others do not germinate readily. Moreover, the mutating species when crossed with other species gives different kinds of plants in the first generation.

All this is evidence that De Vries' primrose is a complex hybrid type, which, because of the poor viability of the seeds, is constantly throwing segregates in small numbers. A parallel case has been found by Muller in Drosophila. As noted before, an organism may be kept in a heterozygous condition by balanced lethals which permit only heterozygotes to live. One lethal in one chromosome kills all individuals of one pure type and a different abnormal gene destroys the other pure type. The hybrid thus breeds true and will continue to do so indefinitely. When crossed with homozygous individuals it may give two types in F_1, like De Vries' primrose, because it always has two different kinds of germ cells. By crossing-over, a lethal factor may be gotten out of one chromosome and a few homozygous, pure-breeding individuals may appear. In this way new types are brought to light, the occurrence of which is similar in every way to the manner in which many of the mutations in other organisms are found to occur. On account of the great complexity which can easily occur in Mendelian phenomena, it must be emphasized strongly that the num-

bers in which new forms appear, however few they may be, is not proof that they are mutations. Without a thorough factor analysis it is impossible to distinguish between mutations and recombinations. As used, the term mutation is given to heritable variations which occur in such a way that no clear reason for their appearance is known. More and more characters, once considered as mutations, are now known to be the result of the normal working of a definite mechanism. All mutations may ultimately be understood as the result of an orderly process. At present, however, we are faced with a type of variation in mutation which is not fully understood, and as far as known, can not be controlled. Such changes are few, and in comparison with the enormous variability made possible by hybridization they are relatively of small practical importance.

Mutations induced by external agencies.—Many attempts have been made to produce changes in germinal construction by outside influences. Solutions of different chemicals have been injected into the ovaries of various plants. A few variations which persisted in their offspring were found, but the frequency of these changes was no greater than in plants not so treated. Guyer and Smith in Wisconsin have employed a far more delicate yet powerful means of altering the germplasm without destroying its power of reproduction. An extract was prepared from the lens tissue of rabbits and injected into the body cavity of fowls. The serum prepared from the blood of such treated birds was injected back into pregnant rabbits. Some of the young born later showed malformations of the eyes, which were transmitted for many generations through the male as well as through the female. It is possible that a specific serum is formed in the treated fowls which has the ability to break down the lens substances and when acting upon the embryonic rabbits not only destroys their eyes but destroys, or renders inactive, that part of the germplasm which produces the eyes. These experiments have not been fully confirmed, and as similar eye defects are common in rabbits

it is not yet certain that specific mutations can be induced by external agencies in this way. Mice were subjected to X-ray treatment at the Carnegie Institution by Little, and, while their immediate offspring were normal, later generations showed decided abnormalities, some of which are inherited as Mendelian recessives. Similar results are reported by Bagg. The organ principally affected is the eye. It may be that, in the serum treatment in the previous experiment, the eye defects are simply the general result of an injurious action. From these experiments, it seems highly probably that the germplasm can be altered by external agencies so that persistent heritable variations can be induced. The changes so far made are destructive and probably are not specific, and while they have no importance as yet for applied genetics, they may mark the beginning of a new epoch in the study of heredity.

Improvement by mutations.—It is well, therefore, to appreciate just what the chances are for obtaining improvement from mutations. Plants propagated vegetatively are usually quite constant. When this means of multiplying plants is used, it is, of course, a sensible procedure to secure parts for propagation from healthy vigorous plants true to the variety wanted, as we have seen. Diseases and the ill effects of an unfavorable environment may be temporarily transmitted from one generation to the next and should always be guarded against. It has been frequently urged that the selection of the best individuals of apples, strawberries, potatoes, and other asexually reproduced plants will lead to a worthwhile improvement. For the most part, experience does not give support to this assumption, as will be brought out more fully in Chapter XIV. The mistaken idea that desirable variations in asexually reproduced plants can be made the basis for improvement by selection comes from the failure to appreciate the fact that such variations are merely modifications due to the environment. Germinal recombination is ordinarily not possible except in sexual reproduction. One can not deny that mutations or

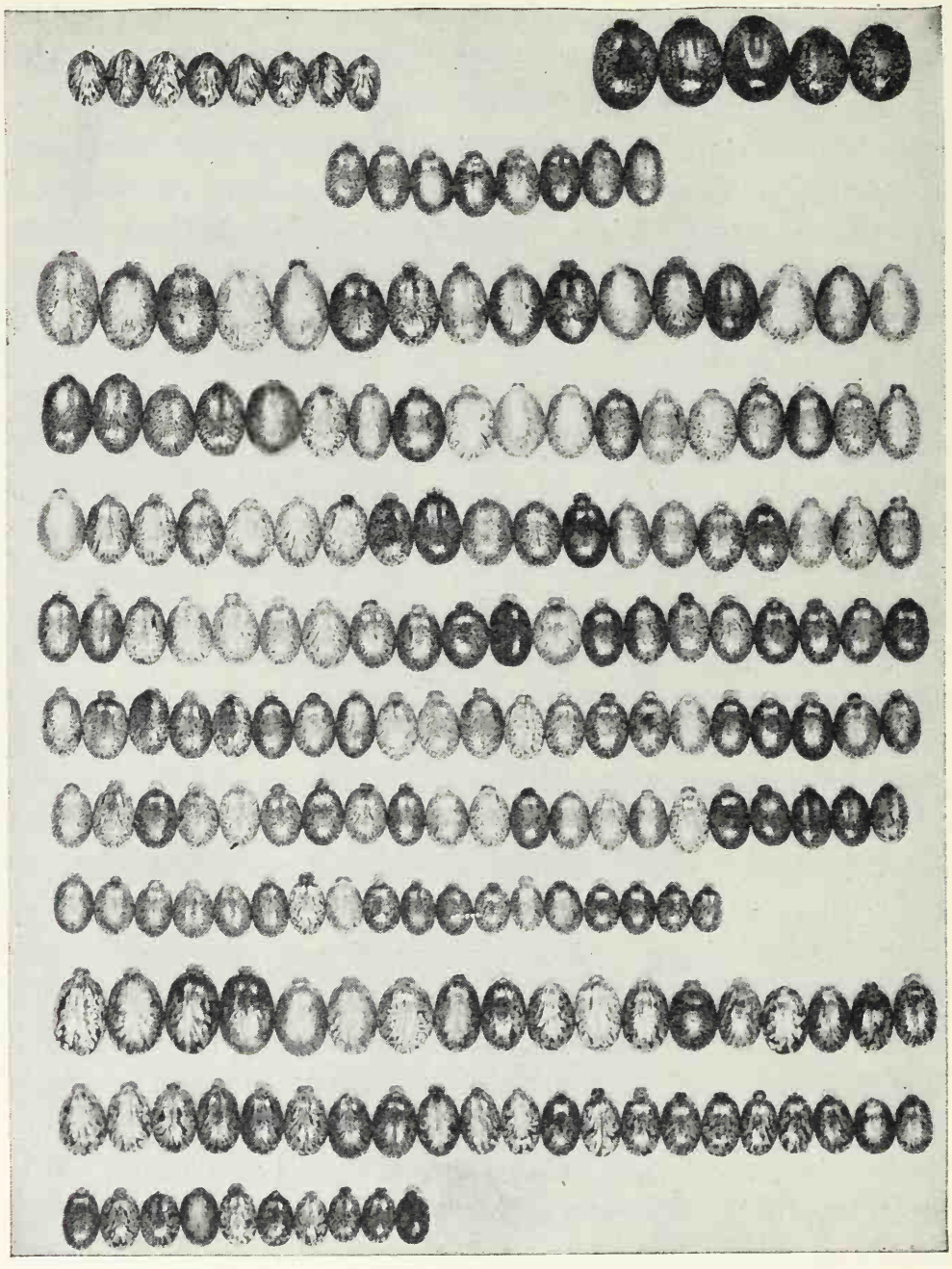


FIG. 85.—Variation in size, color, and markings of castor beans induced by crossing. The two parental types, above; the first generation cross, below; followed by the second generation progeny, one seed from each plant. The fine-mottled and coarse-mottled seeds are arranged in different series. An illustration of continuous variation in size and discontinuous variation in pattern. (After White in Jour. Heredity.)

unusual chromosome combinations of value may occur in vegetatively propagated plants, because there is good evidence that they sometimes do. But so rarely are they found that, in comparison with the enormous and ever-present variability which results from the recombination of hereditary units, mutations are relatively unimportant in the practical business of plant and animal improvement.

Variation due to recombination of germinal units, out of which new forms of value may come, may be illustrated by innumerable examples. In addition to those already given to demonstrate Mendelism, let us take a cross of a small-seeded castor bean with a large-seeded variety, as described by White and shown in Fig. 85. The first generation is uniform in all characters and is intermediate in size as compared with the parental races. The second generation shows an enormous diversity in size, shape, color, and color pattern, ranging from seeds smaller than those of the smaller-seeded parent to seeds larger than those of the other parental variety. The variation in size is continuous or fluctuating Color also intergrades to a certain extent, but the classification with respect to coarse and fine mottling is easily made.

Similar variability induced by crossing is demonstrated in a cross of a short-flowered species of tobacco with a long-flowered species, made by East. The data showing the range in length of corolla of the parents and of the first, second, and third generations are shown in Table X. Note that there is a great range in F_2, and that in F_3 progenies with very different flower lengths were obtained. It is variation of this kind, due to recombination of hereditary units, that makes possible the rapid multiplication of varieties.

In animals, it is readily apparent that many of the distinctive markings of the different breeds are due to simple factor differences. This is well brought out in the comb forms of fowls. Each standard variety is supposed to have only one type of comb, such as Breda or combless,

TABLE X

VARIATION IN LENGTH OF COROLLA IN A CROSS BETWEEN *Nicotiana Langsdorffii* AND *N. Alata*

Data from East, in *Genetics*

Generation	Class Centers in Millimeters																									Number of Plants
	19	22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	
P	23	97	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	120
P	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	8	10	11	8	5	3	1	49
F_1	..	..	..	..	..	1	4	24	16	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	46
F_2	..	2	3	13	65	110	132	107	82	33	15	6	7	0	4	2	..	..	..	..	..	..	..	..	..	..	581
F_3	11	39	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	50
F_3	..	40	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	50
F_3	..	..	..	..	1	24	25	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	50
F_3	..	..	..	..	..	..	1	1	5	12	17	9	11	7	2	1	0	0	0	1	..	..	..	..	..	..	67

single, rose, pea, or walnut, as shown in Fig. 86. Walnut comb results when both dominant factors for pea and rose comb are brought together, and single results when both are lacking. Single differs from combless by one factor. On account of dominance, many carefully selected families continue to produce a few individuals with undesired type of comb.

From this it is evident that many of the differences in size, color, and pattern in farm flocks of poultry are due to diverse combinations of hereditary factors. Where no attention is paid to maintaining a uniform breed, many different types are brought together. The result is a mixture of stock showing great variability in size, shape, comb form, plumage color and pattern. Alley cats and dogs in their particolored patterns and varied hues are the result of indiscriminate mixing of breeds brought from all parts of the world. The result is often bizarre. Such variations are for the most part very complex reassociations of definite hereditary factors which have long been in existence.

Summary.—Variations in animals and plants are therefore to be looked upon as of two general classes: as modifications due to the external surroundings, which are transitory; and changes in the inheritance, which can be

made permanent. Of the latter class, far the larger part are due to different combinations of already formed units or groups of units. But these units themselves are some-

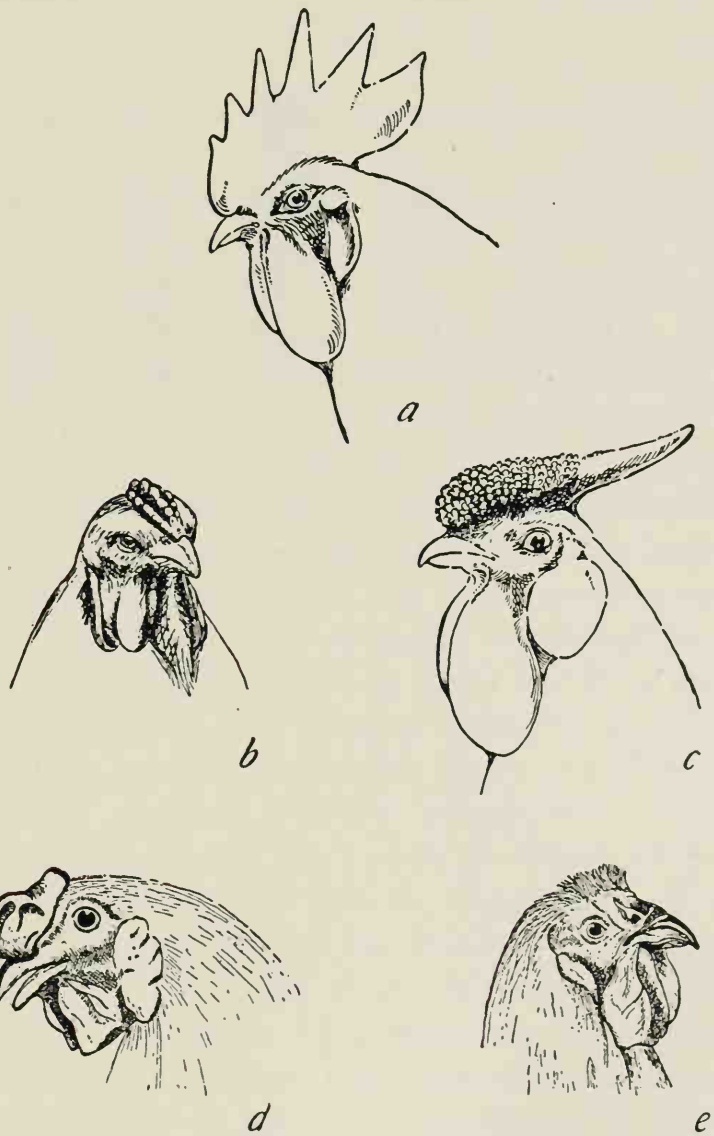


FIG. 86.—Combs of fowls: *a*, single; *b*, pea; *c*, rose; *d*, walnut; *e*, Breda or combless. (After Morgan *et al.* in "Mechanism of Mendelian Heredity," courtesy of Henry Holt & Co.)

times altered to form new ones, which in turn are relatively stable. Such mutations are not produced at will, however, and therefore do not offer the opportunities for the creation of new forms made possible by Mendelian recombinations.

CHAPTER VIII

MEASURING VARIATION AND CORRELATION

In order to distinguish clearly between quantitative variations, which are due to environmental influences and similar deviations which have their basis in hereditary differences, it is necessary to have a measure of diverseness that can be stated in exact terms. For this purpose, certain methods of calculating the amount of variability have been developed.

Statistical classification.—After a number of individuals are measured with respect to any character which varies in a continuous manner, they can be grouped in classes corresponding to the degree to which the character is developed. It will then be found that the way in which the individuals are distributed follows a general plan, which is alike for many characters in many different organisms. This is well illustrated by the figures which Johannsen obtained by measuring the length of seed of the Scarlet Runner bean in studying the inheritance of size differences in this plant. Many seeds were measured and the shortest was found to be 17 mm. and the longest 33 mm. in length. The others ranged between these two extremes. All of the seeds between 17 and 19 mm. in length were put into one class with a mid-class length of 18 mm., all between 19 and 21 in another class represented by 20 mm., and so on for all the figures. Eight groups in all were made, each group being separated by 2 mm. difference in length. The number of seeds which was found to come in these several classes is as follows:

Classes	18	20	22	24	26	28	30	32	millimeters
Frequencies	10	44	122	160	128	64	25	5	number of individuals

The frequency curve.—There is a noticeable tendency for the numbers to be largest in the middle classes, gradually thinning out as the outer limits are reached. This is shown more clearly by putting the seeds of each group in a

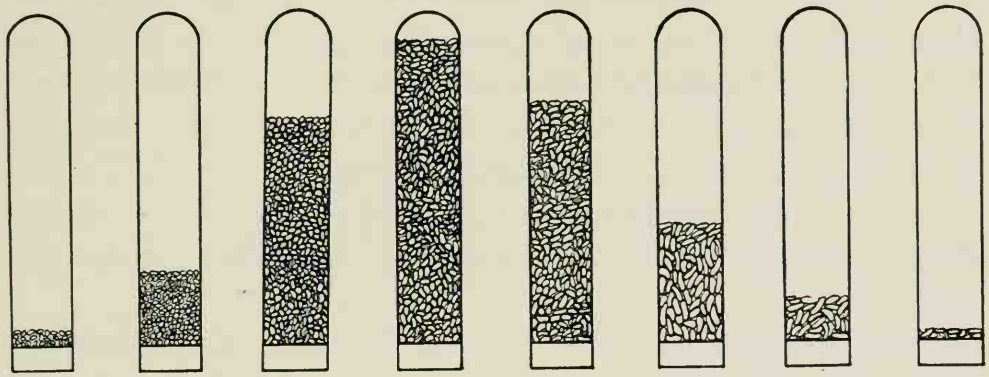


FIG. 87.—Diagram showing the distribution of beans with respect to length of seed. Each tube contains seeds of one length class.

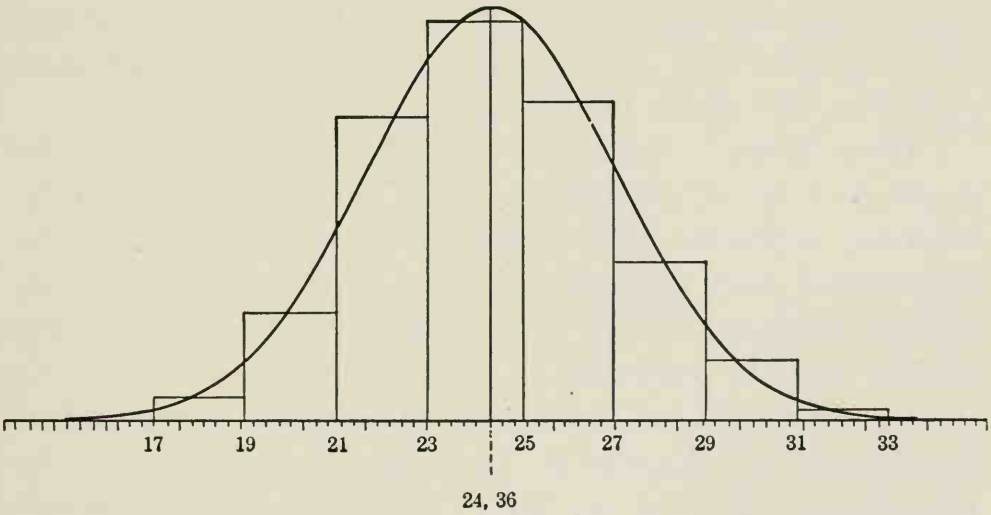


FIG. 88.—Representation by lines of the distribution of bean seeds with respect to length. The height of the columns is proportional to the number of seeds in each class. (After Johannsen in "Elemente der Exakten Erblichkeitslehre," Gustav Fischer.)

glass tube and arranging the tubes in the order of the length of the seeds contained in them as shown in Fig. 87. The same result is shown graphically and more accurately in Fig. 88 by a series of rectangular columns such that the hight of each column is proportional to the number of seeds

which it represents. When the tops of these columns are joined by a line, as shown, the result is a curve. Such a curve is generally used alone, without the columns, to represent, in as simple a form as possible, the distribution of a series of individuals with respect to any measured character. A series of numbers arranged in this fashion is known as a **frequency distribution,** and the diagram which shows at a glance the way in which the individuals arrange themselves is called a **frequency curve.** It shows the frequency of the occurrence of individuals having a certain degree of development with respect to some one measurable character.

The average length of all the seeds in the foregoing illustration is 24.40 mm. and is represented by a line drawn perpendicular to the base at the point on the scale which corresponds to that length. In this case, as is usually the result, there are more beans of average length than of any other length, and the remaining numbers are grouped symmetrically about the middle class.

These figures, obtained from a living organism, can be duplicated in a remarkably close manner by a purely mechanical process, such as tossing coins and observing the frequencies with which the various combinations of heads and tails appear. When two coins are tossed, the following results may be expected: (1) head head, (2) head tail, (3) tail head, (4) tail tail. Any one of these combinations is equally likely to appear, provided the coins are exactly alike and are thrown entirely at random. The second and third classes, being alike, can be grouped together so that the most probable result of 4 throws of 2 pennies each time, is

$$1HH+2HT+1TT$$

Similar, the best bet with 3 coins in 8 throws is

$$1HHH+3HHT+3HTT+1TTT$$

With two coins, HT occurs twice as often on the average as HH or TT; and with three coins, HHT is three times as

likely to appear as HHH or TTT in any single throw. With ten coins, the relative probability of obtaining any combination of heads and tails is shown in Table XI.

TABLE XI

THE RELATIVE PROBABILITY OF OBTAINING VARIOUS COMBINATIONS OF HEADS AND TAILS IN THROWS OF TEN COINS

Heads	Tails	Relative Probability
10	0	1
9	1	10
8	2	45
7	3	120
6	4	210
5	5	252
4	6	210
3	7	120
2	8	45
1	9	10
0	10	1
		1024

These values are represented graphically in Fig. 89. The similarity of this distribution to the results obtained by Johannsen with seeds is apparent.

Mean, mode, and median.—The three series, from 2, 3, and 10 coins, can be obtained by expanding the binomial expressions $(1+1)^2$, $(1+1)^3$, $(1+1)^{10}$. The probabilities of all the combinations, when any number of coins are tossed at the same time, can be calculated by expanding $(1+1)^n$. When n becomes indefinitely large the curve approaches the form shown in Fig. 90. This is known as the **normal probability curve.** It is perfectly symmetrical, and the longest straight line that can be drawn within the curve, perpendicular to the base, divides the area into two equal parts. This line, designated as M in the illustration, represents three important determinations which can be

calculated from a frequency distribution of this kind. These are the **mean,** the **mode,** and the **median.**

The **mean** is the arithmetical average of all the individ-

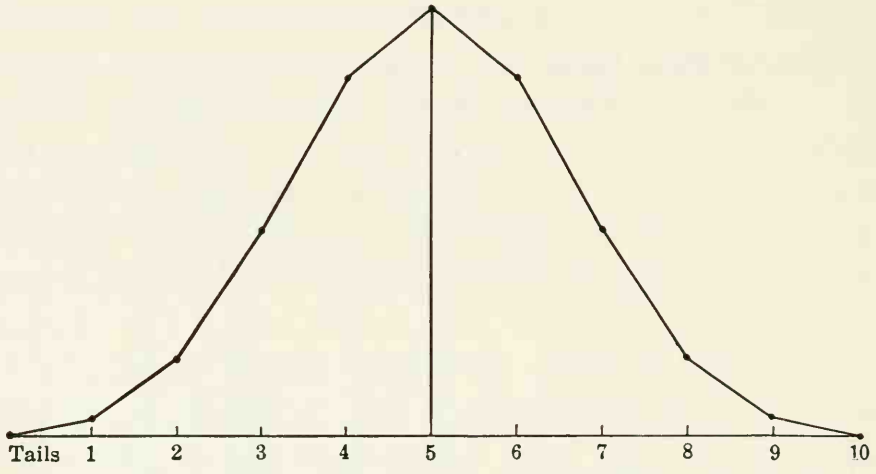


FIG. 89.—Graphical representation of the probabilities given in Table XI. (After Lock in "Variation, Heredity and Evolution," John Murray.)

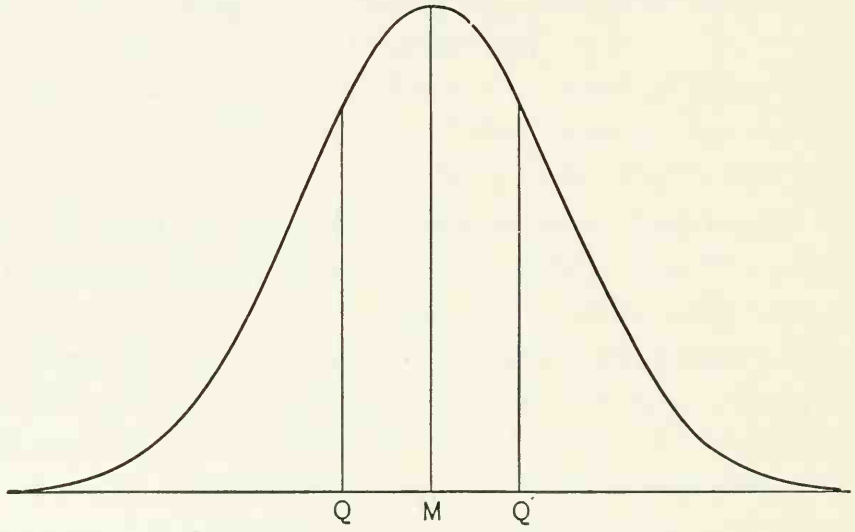


FIG. 90.—The normal probability curve. *M*, mean, mode, and median; *Q*, *Q'*, the two quartiles. (After Lock in "Variation, Heredity and Evolution," John Murray.)

uals included in the distribution and is obtained simply by multiplying the value of each class by the number of individuals contained in that class. The sum of these products divided by the total number of individuals gives the mean,

or average. The **mode** is that class which contains the greatest number of individuals and gets its name from the fact that it is the most fashionable group. The **median** is the magnitude that divides all the individuals into two lots of equal numbers, so that half the individuals show the same or greater development than the median and the other half show the same or less development of the character measured.

In the graphical representation by curves, the mean, the mode, and the median are represented by straight lines erected perpendicular to the base at the points corresponding to their values. In a perfectly symmetrical distribution, such as the theoretical curve shown in Fig. 90, the three points coincide, so that the one line, *M*, represents all three. In a distribution which is not exactly symmetrical the three values do not coincide, but they are not widely separated in any distribution of this general type.

The measure of variability.—The shape of the frequency curve gives some idea of the variability of the group from which the measurements are taken. Thus, with curves from two different lots having equal numbers and plotted on the same scale, the curve that has the lesser height and greater spread would represent a greater variability. This is evident for the reason that variation is simply the deviation of certain numbers of individuals from the mean condition. Proportionally greater numbers in the outer classes than in the center classes indicate lesser conformity to type. Therefore, a mathematical measure of variability must be a representation of the spread of the frequency curve.

There are two simple measures of variability. These are the **average deviation** and the **standard deviation.** The first is merely an average of all the deviations from the mean. It is calculated, as shown in Table XII, by first obtaining the mean, finding the deviations of each class from this mean, and then multiplying the deviation of each class by the number of frequencies in that class. The sum

TABLE XII

CALCULATION OF MEAN, AVERAGE DEVIATION AND STANDARD DEVIATION OF LENGTH OF SEED OF SCARLET RUNNER BEANS

Data from Johannsen

Mid-class Values mm. v	Frequencies f	Frequencies × Class Values $f \cdot v$	Deviations from Mean mm. d	Deviations × Frequencies $f \cdot d$	Deviations Squared d^2	Deviations Squared × Frequencies $f \cdot d^2$
18	10	180	6.4	64.0	40.96	409.60
20	44	880	4.4	193.6	19.36	851.84
22	122	2684	2.4	292.8	5.76	702.72
24	160	3840	.4	64.0	.16	25.60
26	128	3328	1.6	204.8	2.56	327.68
28	64	1792	3.6	230.4	12.96	829.44
30	25	750	5.6	140.0	31.36	784.00
32	5	160	7.6	38.0	57.76	288.80
	558	13614		1227.6		4219.68

number of measurements $n = 558$

$$\text{mean} = \frac{\Sigma f \cdot v}{n} = \frac{13614}{558} = 24.398 \; mm$$

$$\text{average deviation} = \frac{\Sigma f \cdot d}{n} = \frac{1227.6}{558} = 2.20 \; mm$$

$$\text{standard deviation} = \sqrt{\frac{\Sigma f \cdot d^2}{n}} = \sqrt{\frac{4219.68}{558}} = 2.75 \; mm$$

of these products divided by the total number of individuals is the average deviation. The average deviation is not as good a measure of variability as the standard deviation, which is calculated by first squaring the deviations, before multiplying by the frequencies, and then extracting the square root of the sum of the products after dividing by the total number of individuals. This is shown in detail in Table XII.

The short method of calculating the mean and standard deviation.—A quicker and more accurate method of calculation is shown in Table XIII. After the data are arranged in the frequency distribution, an assumed mean is taken arbitrarily. This may be taken at any point. The deviations will be the least if the mean is assumed to be near

reliable measure of variation than the average deviation, because it is based on the method of least squares. This may be made clear by an illustration of two riflemen shooting at a target marked with rings uniformly spaced one foot apart from the center out. Let the two riflemen, A and B, each shoot twice, with the result shown in Fig. 91. A lands both of his shots in circle 2, while B hits within circle 1 and 3. Which is the better marksman? If we simply add the two scores, with the understanding that the smaller score indicates the better shooting, we find that they both shot equally well. A has $2+2=4$ and B $1+3=4$. It is clear, however, that A is a more consistent hitter as his shots are less scattered than those of B. Moreover, A required less total area to hit the target than did B. Since the area of a circle is equal to πr^2, the area A required for both shots is twice $\pi 2^2$, while B needed $\pi 1^2+\pi 3^2$ to land his shots. These two areas stand in the ratio of 8 to 10. Therefore, if the scores are first squared, then added, and the square root extracted from their sum, we have for A $\sqrt{2^2+2^2}=\sqrt{8}$ or 2.83, and for B $\sqrt{1^2+3^2}=\sqrt{10}$ or 3.16, and therefore A is the winner. Since variability is the amount of deviation from the mean of all the individuals under observation, the principle of least squares applies to variation of all kinds.

the middle of the distribution. In this case the 24 mm. class is taken as the assumed mean length of seed. The deviations by classes from this assumed mean are then entered in the column headed d'. These are multiplied by the frequencies, and their algebraic sum, +111, divided by the total number of individuals, 558, gives the correction, +.199. This correction, after being multiplied by the class interval, 2, is added or subtracted from the assumed mean according to its sign to give the true mean, 24.398. The products of the deviations by the frequencies, fd', are again multiplied by the deviations, d', to give the frequencies by the deviations squared, fd'^2. From their sum, 1857, divided by n, is subtracted the correction squared. The

TABLE XII

CALCULATION OF MEAN, AVERAGE DEVIATION AND STANDARD DEVIATION OF LENGTH OF SEED OF SCARLET RUNNER BEANS

Data from Johannsen

Mid-class Values mm. v	Frequencies f	Frequencies × Class Values $f \cdot v$	Deviations from Mean mm. d	Deviations × Frequencies $f \cdot d$	Deviations Squared d^2	Deviations Squared × Frequencies $f \cdot d^2$
18	10	180	6.4	64.0	40.96	409.60
20	44	880	4.4	193.6	19.36	851.84
22	122	2684	2.4	292.8	5.76	702.72
24	160	3840	.4	64.0	.16	25.60
26	128	3328	1.6	204.8	2.56	327.68
28	64	1792	3.6	230.4	12.96	829.44
30	25	750	5.6	140.0	31.36	784.00
32	5	160	7.6	38.0	57.76	288.80
	558	13614		1227.6		4219.68

number of measurements $n = 558$

$$\text{mean} = \frac{\Sigma f \cdot v}{n} = \frac{13614}{558} = 24.398 \text{ mm}$$

$$\text{average deviation} = \frac{\Sigma f \cdot d}{n} = \frac{1227.6}{558} = 2.20 \text{ mm}$$

$$\text{standard deviation} = \sqrt{\frac{\Sigma f \cdot d^2}{n}} = \sqrt{\frac{4219.68}{558}} = 2.75 \text{ mm}$$

products divided by the total number of individuals

FIG. 91.—A target with rings uniformly spaced from the center. *A* lands two shots in circle 2; *B* lands his two shots in circles 1 and 3. Which is the better marksman?

easier to make the calculation this way, but, owing to the elimination of decimals, the method is often more accurate and should always be used. A convenient method of checking the calculation is given in the last column of Table XIII. For each class the values of $f(d'+1)^2$ are found. For example, in the first class $10(-3+1)^2 = 40$. The sum of $f(d'+1)^2$ equals the sum of f, plus the sum of $2fd'$, plus the sum of fd'^2.

The standard deviation is mathematically a more

reliable measure of variation than the average deviation, because it is based on the method of least squares. This may be made clear by an illustration of two riflemen shooting at a target marked with rings uniformly spaced one foot apart from the center out. Let the two riflemen, *A* and *B*, each shoot twice, with the result shown in Fig. 91. *A* lands both of his shots in circle 2, while *B* hits within circle 1 and 3. Which is the better marksman? If we simply add the two scores, with the understanding that the smaller score indicates the better shooting, we find that they both shot equally well. *A* has $2+2=4$ and *B* $1+3=4$. It is clear, however, that *A* is a more consistent hitter as his shots are less scattered than those of *B*. Moreover, *A* required less total area to hit the target than did *B*. Since the area of a circle is equal to πr^2, the area *A* required for both shots is twice $\pi 2^2$, while *B* needed $\pi 1^2+\pi 3^2$ to land his shots. These two areas stand in the ratio of 8 to 10. Therefore, if the scores are first squared, then added, and the square root extracted from their sum, we have for *A* $\sqrt{2^2+2^2}=\sqrt{8}$ or 2.83, and for *B* $\sqrt{1^2+3^2}=\sqrt{10}$ or 3.16, and therefore *A* is the winner. Since variability is the amount of deviation from the mean of all the individuals under observation, the principle of least squares applies to variation of all kinds.

Coefficient of variation.—The standard deviation, S. D., is expressed in the units in which the measurements are taken. In the case of seed length, the S. D. of this particular lot is 2.75 mm. If we wish to compare the variability in length with the variability in weight or with the variability of any other character of the same or different organisms, it is necessary to state the deviation in its relation to the mean. The percent which the standard deviation is of the mean is known as the **coefficient of variation.** This coefficient, C. V., is calculated from the standard deviation by the formula

$$\text{C. V.} = \frac{100 \text{ S. D.}}{\text{mean}}$$

The coefficient of variability is used in studying the inheritance of quantitative characters. Thus in the two varieties of corn, which differed in length of ear, crossed by East with the results shown in Table VI (page 80) the small-eared variety ranged from 5 to 8 cm. in length while the larger variety varied from 13 to 21. As shown in Table XIV, the first-generation hybrid was intermediate in

TABLE XIV

THE MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION IN LENGTH OF EAR OF CORN FROM A CROSS OF A SHORT AND LONG-EARED VARIETY

Data from East, in *American Naturalist*

Generation	Number of Plants	Mean Length	Standard Deviation	Coefficient of Variation
P	57	6.6±.07	0.8±.05	12.3±.78
P	101	16.8±.12	1.9±.09	11.1±.53
F_1	69	12.1±.12	1.5±.09	12.5±.72
F_2	221	12.6±.13	2.8±.09	22.3±.74

length compared with its two parents and was no more variable, as shown by the coefficients of variation. The second generation, however, was far more variable, the coefficient being nearly twice as large as for the first generation. Although greater numbers were grown in this last generation it can be seen that they are not distributed in the same way. The central classes contain proportionally less than the outer classes as compared with the other generations. The difference in variability between the first and second generations is therefore a measure of the hereditary control over ear length, since the environmental causes of variation were equal in each case.

Probable error.—It is also necessary to have a measure of the amount of variation in order to know the reliability of a determination based upon a number of variable individuals. Returning to the normal probability curve shown in Fig. 90, it will be seen that there are two lines

marked Q, which divide each half of the enclosed area. These are known as the **quartiles** and represent the points on the base line at which two perpendiculars can be erected which, together with the median, divide the total area into four equal parts. In a symmetrical curve the two quartiles are equally distant from the median. This distance, given in the units in which the measurements are taken, is known as the **quartile deviation.** One half of the total number of individuals represented by a curve lie within, and one half without, the area enclosed by the two quartiles. The chances are therefore equal that any single individual taken at random will or will not deviate from the middle class more than the quartile deviation. Upon this fact is based the determination of the probable deviation or **probable error,** as it is technically called. The probable error is a measure of reliability and shows how much a calculation based on a limited number of individuals may reasonably differ from the true value based upon all the individuals of the same kind in existence.

The term probable error is used in a special sense and has nothing to do with the actual error. Mistakes often occur in making measurements and carrying out the calculations. Small errors of this kind, if they occur at random, tend to counterbalance each other and are not so serious as the common source of error which comes from not having a truly representative sample. Most statistical fallacies arise in this way, and although the mathematical treatment of the material is entirely correct the conclusions drawn from the data may be wholly misleading.

Requisites for reliability.—The value of any determination, such as the mean, standard deviation, and coefficient of variation, based upon a limited number of measurements, depends upon several conditions:

1. *Random sample.*—The individuals measured must be representative. Differences due to environmental influences and age must be taken into account. The mixing of different kinds of materials must be avoided. The individ-

uals included in the sample that is measured must be taken as they come, without rejecting or selecting any because of their development in the character to be measured or in any other features that may be directly or indirectly associated with this character.

2. *Variability.*—The more variable the material is, the less likelihood there is that two samples from the same material will give the same result.

3. *Numbers.*—The more individuals are included in the measurements, other things being equal, the less chance there is that the sample will differ from the entire lot. However, the reliability of a determination does not increase directly with the numbers used but as the square root of the numbers.

Calculating the probable error.—The probable error depends entirely upon the amount of variability and the numbers employed. The probable error of a single measurement is the quartile value of the group from which it is taken. The probable error for the entire group is the quartile divided by the square root of the numbers contained within the group. The quartile in the theoretically normal curve can be easily calculated from the standard deviation by multiplying that result by 0.6745. Therefore the formula for the probable error of the mean is

$$E_M = 0.6745 \frac{\text{S. D.}}{\sqrt{n}}$$

This method of calculating the probable error is not strictly accurate for distributions that are not perfectly symmetrical, but is sufficiently reliable for most practical purposes. The probable error of other determinations, such as the standard deviation and coefficient of variability, is calculated from somewhat different formulas, but is based upon the same principle.[1]

[1] For these formulas and their application the reader is referred to Davenport's "Statistical Methods," John Wiley & Sons, and Yule's "Introduction to the Theory of Statistics," J. B. Lippincott Co.

Applying the probable error.—The probable error indicates the amount by which a determination based upon limited numbers may vary from the true value for all the individuals of that kind. In other words, the chances are even that the true value lies between the determination found plus the probable error and the same value minus the probable error. The chances that the true value may differ by an equal or greater amount than the probable error are as follows:

±1E chances are	1.0 to 1
±2E chances are	4.5 to 1
±3E chances are	21.0 to 1
±4E chances are	142.0 to 1
±5E chances are	1310.0 to 1
±6E chances are	19200.0 to 1
±7E chances are	420000.0 to 1
±8E chances are	17000000.0 to 1

It is arbitrarily considered that three times the probable error is the limit by which two determinations may vary and still be chance deviations from the true value. For example, Johannsen found that his Scarlet Runner beans, which had an average length of 24.40 mm. gave a probable error of ±0.079 mm. Necessarily, only a relatively small number of seeds were measured. If an infinitely large number of seeds of the same variety, grown under the same conditions, were measured, many of them would differ in length from the average of the sample already measured but the chances are even that none of them would be longer than 24.40+.079, i.e., 24.479, or shorter than 24.40−.079, i.e., 24.321. The average length of seed in Johannsen's case is therefore given as 24.40±.079 mm. If another lot of seeds of this type differed in average length by more than three times the probable error of the difference [2] it would be reasonable to suppose that the plants which produced these seeds were genetically different from the former stock or were subjected to different environmental

[2] The probable error of the difference of two numbers is the square root of the sum of the probable errors of the two numbers.

influences during growth. The results could not be considered as chance deviations from a common true mean.

Usefulness of the probable error.—To illustrate the important use to which the probable error is put in dealing with problems in genetics, let us take an illustration furnished by tobacco. The indeterminate non-flowering type of tobacco, which was described in the previous chapter as an example of mutation in a single factor, was crossed with the variety from which it originated. All of the first-generation plants flowered and produced seed, but had a higher average number of leaves than the flowering parent. The second generation gave some plants that flowered and some that did not. The distribution of leaf numbers of the flowering plants indicated that they were of two types. One type was composed of homozygous dominant individuals which were a return to the flowering parental type, and the other was composed of heterozygous dominants which reduplicated the F_1 plants. Several F_3 progenies were grown, and the data for leaf numbers of these plants compared with the first, second, and parental generations are shown in Table XV. All the plants were grown under the same conditions. As there is no basis for comparing

TABLE XV

DISTRIBUTION AND VARIABILITY OF LEAF NUMBER OF TOBACCO IN A CROSS BETWEEN A DETERMINATE AND AN INDETERMINATE GROWTH TYPE

Generation	Number of Leaves of Determinate Plants												Number of Plants	Average Number of Leaves	Coefficient of Variation
	19	20	21	22	23	24	25	26	27	28	29	30			
P	..	8	18	15	4	..	..	..	..	..	..	..	45	21.3±.09	4.1±.29
F_1	..	..	..	..	..	16	18	14	10	2	..	..	60	25.4±.10	4.5±.28
F_2	..	4	13	12	9	6	11	10	11	7	..	..	83	24.0±.18	10.2±.53
F_3	5	21	37	22	5	..	..	..	..	..	..	..	90	21.0±.07	4.6±.23
F_3	..	..	11	17	8	8	15	10	11	5	1	1	87	24.3±.17	9.5±.49
F_3	..	..	3	16	16	8	7	16	3	7	1	1	78	24.4±.17	8.9±.48

the non-flowering plants, they are omitted. The average leaf number of the original variety A is 21.3±.09 and the same determination for the one F_3 progeny that has a similar distribution is 21.0±.07. Since the difference of the two averages is less than either probable error, this can be taken as an indication that the two lots are genetically alike. Similarly the variability in leaf number, as measured by the coefficient of variation, is 4.1±.29 and 4.6±.23 in the two cases, a difference which is less than twice the probable error of the difference.

Comparing the average leaf number of the two F_2 and the two segregating F_3 progenies, the greatest difference is less than twice the probable error. Variability likewise is well within the limits commonly set for chance deviations. It is therefore justifiable to conclude, as far as this evidence goes, that the germinal variation was a single factor change from the original condition.

Take another case in which it is necessary to compare the weights of self-fertilized and cross-fertilized seeds pro-

TABLE XVI

Distribution with Respect to Weight of Self-fertilized and Cross-fertilized Seeds of Corn Grown in the Same Inflorescences

Class	Weight of Seeds Cgs.									Number of Seeds	Average Weight of Seeds	Increase in Weight
	10	14	18	22	26	30	34	38	42			
A	..	..	..	1	7	53	11	1	..	73	30.2±.19	5.7±.25
A×B	..	..	1	0	3	12	72	90	10	188	35.9±.16	
B×A	..	..	..	6	33	5	..	..	..	44	25.9±.20	4.2±.26
B	1	1	2	63	2	..	..	..	..	69	21.7±.16	

duced in the same inflorescences of maize. The seeds resulting from the application of a mixture of pollen to two different types of plants and their weights are given in Table XVI. The two lots of seeds were distinguished by

differences in color of endosperm. Since the seeds were scattered at random over the ears and developed under as nearly equal environmental conditions as is possible to have, any difference in average weight of seed, if significant, must be due to the effects of crossing.

The self-fertilized seeds in one case averaged $30.2 \pm .19$ centigrams, whereas the cross-fertilized seeds gave a mean value of $35.9 \pm .16$. The difference in favor of the crossed seeds is $5.7 \pm .25$ or nearly 23 times the probable error of the difference. Similarly, the reciprocally crossed seeds differ from the self-fertilized seeds grown with them by $4.2 \pm .26$ cg., which is an increase of 16 times the probable error. The chances that these differences are merely random departures from a common mean are so extremely small that there can be no reasonable doubt that the differences are significant and that crossing in this case has a noticeable influence in increasing the weight of seed.

Limitations of the probable error.—It should be remembered, however, that the probable error is calculated from a purely empirical formula and while it is applicable to many biological problems it is not necessarily dependable in every case. A good illustration of the questioned reliability of the probable error is furnished by Stewart. A large number of seed potato tubers were divided lengthwise into two equal parts. Each pair was planted close together and evenly spaced and the plants from every half tuber harvested separately. The average yield of one set of 429 half tubers was greater than the remaining paired set by a difference of $1.1 \pm .26$ ounces. This difference is 4.2 times the probable error. This would indicate that the chances are about 190 to 1 that the true value of the difference is somewhere between 1.36 ($1.1 + 0.26$) and 0.84 ($1.1 - 0.26$) ounces. Yet there is no conceivable reason why there should be any significant difference in the two averages. With larger numbers the difference should approach zero. This emphasizes the fact that the influences which affect the growth of living organisms are so numerous and complex that it is

extremely difficult to secure even reasonably comparable results, and that in drawing conclusions from biological experiments the probable error is not absolutely reliable and can never take the place of a careful and impartial examination of the results from all possible viewpoints.

Correlated variability.—Having developed a measure of variability, and from that a method of estimating the reliability of averages based upon a number of variable quantities, the next step in biological mathematics, or biometry as this subject is now called, is to have a means of calculating the amount of correlation between two different variable characters.

There are numerous cases in which the development of a certain character in one part of the animal or plant is associated with a corresponding development in other parts of the same individual. In many plants, color in the stems and foliage regularly accompanies coloration of the flower. Thus, with the garden nasturtium, plants with dark-colored stems and leaves have dark-colored flowers. In albino variations, which occur in many animals, no color is developed in the hair, and the same individuals regularly lack pigment in the eyes, the result being that a pink color from the blood vessels shows through the uncolored transparent membranes.

Partial correlation.—Such characters as these, being always associated in certain ways, are perfectly correlated. Other characters which show fluctuating variation are not perfectly correlated, but the development in some parts is accompanied by a corresponding tendency to develop other parts. It is obvious that most size characters will show such a relation. Tall individuals are, as a rule, heavier than short ones. Long bones in one part of the body are accompanied by long bones in other parts. Large plants are usually more productive than small plants. Such correlations are to be expected, since heredity and environment affect the whole organism in the same way to a greater or less degree.

Use of correlations.—Where easily seen characters are associated with the development of desirable qualities that are difficult to evaluate, correlations may be useful in selection. Desirable plants can be saved and undesirable plants rogued out, sometimes in the early seedling stage, by using certain characters by which they can be identified. For example, Parker finds, in sorghum crosses made at the Kansas Station, that juicy and dry stalks are always associated with a translucent or opaque appearance of the midrib of the leaves. Hedrick, from observations at the Geneva Station, states that grape seedlings with short internodes have compact bunches of fruit whereas long internodes, which are apparent before the vines come into bearing, are associated with a loose and undesirable type of fruit cluster. Since the grape inflorescence is a modified branch, it is not difficult to see why this correlation should hold.

When dealing with those characters which are not perfectly correlated, it is necessary to know the degree to which correlation is actually shown. When there is a high degree of association, it can usually be estimated by inspection; but judgment is often faulty, and an exact statistical calculation of the amount of correlation is the only sure means by which selection can be carried on with certainty.

When the score-card method of judging seed corn was first proposed, it was assumed that certain ear characters were associated with high yield in the plants grown from that seed. Extensive investigations have shown that this is not so. Some originators of new varieties of fruit trees are positive that they can recognize, in the seedling stage, valuable features of yield and quality of the mature tree. If selection could be made with seedlings, by means of characters such as internode length in grapes, for example, this would greatly reduce the cost of producing valuable new varieties, since it takes several years for fruit trees to come into bearing. However, in most cases correlations have not been proved statistically. Ballard has followed

apples and pears from seedlings to bearing age at the Maryland Station without being able to find any consistent correlations of value. Similarly animal husbandry men have placed too much reliance upon assumed correlations between body markings and production, particularly in dairy cattle. Extensive statistical investigation has failed to show that correlations exist which are high enough to have practical value. It is therefore essential that all assumed correlations be adequately tested statistically.

Calculating the amount of association.—Where individuals can be classified according to the presence or absence of two alternative pairs of characters, there is a simple method of calculating the degree of association. For example, in a cross between a tunicate variety of maize (pod corn in which each seed is enclosed by husks) having smooth, starchy seeds, and a normal-eared variety with wrinkled, sweet grains, there was found in the second generation an association between tunicate ear and starchy seed on the one hand, and between normal ear and wrinkled seed on the other. The actual results were 113 plants with tunicate ears grown from starchy seed and 4 non-tunicate plants from the same kind of seed. In contrast to this, from the wrinkled, sweet seeds there were obtained only 7 plants with tunicate ears while there were 25 normal-eared plants from this kind of seed. In other words, the grandparental combinations of characters tended to stay together while the new combinations were few. The amount of association is calculated after the plants have first been classified in two ways: for the presence or absence of starchy seeds, and for the presence or absence of tunicate ears. The figures arranged in this way are as follows:

	Starchy	Not Starchy
Tunicate	113	7
Not Tunicate	4	25

The measure of association between starchy seeds and tunicate ears is expressed by

$$\frac{(113\times25)-(7\times4)}{(113\times25)+(7\times4)}=+0.98$$

This is Yule's Coefficient of Association. The general formula by which it is calculated is stated as follows:

$$\frac{ad-bc}{ad+bc}$$

where *abcd* is the number of individuals in a group which can be classified with reference to the presence or absence of two characters, *M* and *N*, as follows:

	M present	*M* absent
N present	*a*	*b*
N absent	*c*	*d*

Whenever *ad* is equal to *bc*, the coefficient of association is zero. When *ad* is greater or less than *bc*, the coefficient is plus or minus. When either *ad* or *bc* is zero, the association is complete and equal to 1; otherwise the coefficient ranges between +1 and −1. In the illustration given, the association +0.98 is high, indicating that the factors controlling these two characters are located in the same chromosome and near each other. If no linkage were shown, the ratio would be approximately 9 : 3 : 3 : 1 which would give

$$\frac{(9\times1)-(3\times3)}{(9\times1)+(3\times3)}=0$$

Calculating correlation.—Not all characters which show association can be classified in this simple manner. For example, Johannsen found that the heavier seeds of barley tended to have a higher percent of nitrogen. In this case there is a correlated variability such that a tendency to

vary in one direction is accompanied by a tendency to vary in another direction. The first step in the calculation of the degree of correlation between two variable characters such as these is to make a correlation table, as shown in Table XVII. In this case, seed from a number of spikes

TABLE XVII

CORRELATION TABLE SHOWING A POSITIVE ASSOCIATION BETWEEN WEIGHT OF SEED OF BARLEY AND THE PERCENT OF NITROGEN IN THE SEED

Data from Johannsen

Weight Seed	Percent Nitrogen 1.2	1.4	1.6	1.8	2.0	
42.5		1				1
47.5	4	15	2			21
52.5	5	49	25			79
57.5		18	30	7		55
62.5			10	4	2	16
67.5				1		1
	9	83	67	12	2	173

of barley are weighed and averaged and the same lots of seed are also analyzed for nitrogen. Each spike is then entered in the table according to the vertical class into which it falls with respect to nitrogen content and the horizontal class with respect to seed weight. For example, there are 15 spikes whose average weights of grain are between 45 and 50 milligrams, and which also have a nitrogen percentage between 1.3 and 1.5. In a correlation table the numbers are distributed in two directions, instead of one as in the simple frequency distribution.

An examination of the table shows that, in general, there is a marked tendency for the lighter seeds to have a lower content of nitrogen while the heavier seeds are inclined to be higher in percent of this ingredient. The correlation is not perfect, because the individuals in one

class with respect to weight are not all in one class with respect to chemical composition. However, the association is high and is also positive, because the individuals that are above the average in weight are also, as a rule, above the average in content of nitrogen.

Table XVIII shows a similar distribution of seed weight

TABLE XVIII

CORRELATION TABLE SHOWING A NEGATIVE ASSOCIATION BETWEEN WEIGHT OF SEED OF OATS AND THE PERCENT OF OIL IN THE SEED

Weight Seed	Percent Oil: 4.75	5.25	5.75	6.25	6.75	7.25	7.75	8.25	
32.5					8	2	1		11
37.5		1	6	22	33	10	2	1	75
42.5	1	2	10	48	37	8	1		107
47.5		1	12	11	2				26
52.5		2	1	1					4
57.5			1						1
	1	6	30	82	80	20	4	1	224

and oil content in oats, in which the correlation is negative. Here the individuals that are above the average in weight tend to be below the average in percent of oil. The two results are nearly the same in amount, but in one case the correlation is positive and in the other negative. Negative and positive correlations are equally useful, because it makes no difference how the characters are associated as long as an actual association exists.

The coefficient of correlation.—From data of this kind a mathematical measure of the amount of correlation can be obtained, as worked out by Pearson. This is known as the **Coefficient of Correlation,** and its calculation can be illustrated as shown in Table XIX, where some of the figures obtained from barley are used. Here the correlation is calculated without arranging the measurements in the form

TABLE XIX

SIMPLE METHOD OF CALCULATING THE CORRELATION COEFFICIENT ILLUSTRATED BY SOME OF THE FIGURES ON WEIGHT OF SEED OF BARLEY AND PERCENT OF NITROGEN IN THE SEED GIVEN IN TABLE XVII

Data from Johannsen

Analysis Number	Nitrogen Percent x	Seed Weight y	Deviation from Average		Product $d_x \times d_y$		Deviation Squared	
			d_x	d_y	Positive	Negative	d_x^2	d_y^2
1	1.71	66.0	+0.236	+11.52	2.719	.....	0.0557	132.7102
2	1.57	62.4	+0.096	+7.92	0.760	.....	0.0092	62.7264
3	1.66	58.8	+0.186	+4.32	0.804	.....	0.0346	18.6624
4	1.52	53.4	+0.046	−1.08	.....	0.050	0.0021	1.1664
5	1.36	51.1	−0.114	−3.38	0.385	.....	0.0130	11.4244
6	1.41	51.2	−0.064	−3.28	0.210	.....	0.0041	10.7584
7	1.29	49.0	−0.184	−5.48	1.008	.....	0.0339	30.0304
8	1.31	51.2	−0.164	−3.28	0.538	.....	0.0269	10.7584
9	1.45	55.2	−0.024	+0.72	.....	0.017	0.0006	0.5184
10	1.42	55.3	−0.054	+0.82	.....	0.044	0.0029	0.6724
11	1.31	48.5	−0.164	−5.98	0.981	.....	0.0269	35.7604
12	1.44	52.4	−0.034	−2.08	0.071	.....	0.0012	4.3264
13	1.31	54.8	−0.164	+0.32	.....	0.052	0.0269	0.1024
14	1.33	51.8	−0.144	−2.68	0.386	.....	0.0207	7.1824
15	1.74	59.6	+0.266	+5.12	1.362	.....	0.0708	26.2144
16	1.51	56.8	+0.036	+2.32	0.084	.....	0.0013	5.3824
17	1.67	53.4	+0.196	−1.08	.....	0.212	0.0384	1.1664
18	1.39	54.8	−0.084	+0.32	.....	0.027	0.0071	0.1024
19	1.49	51.8	+0.016	−2.68	.....	0.043	0.0003	7.1824
20	1.45	51.8	−0.024	−2.68	0.064	.....	0.0006	7.1824
21	1.53	55.4	+0.056	+0.92	0.052	.....	0.0031	0.8464
22	1.24	51.0	−0.234	−3.48	0.814	.....	0.0548	12.1104
23	1.41	54.6	−0.064	+0.12	.....	0.008	0.0041	0.0144
24	1.45	50.2	−0.024	−4.28	0.103	.....	0.0006	18.3184
25	1.87	61.4	+0.396	+6.92	2.740	.....	0.1568	47.8864
Sum	36.84	1361.9			13.081 +12.628	−0.453	0.5966	453.2060

of a correlation table. This is a more simple process and shows the principles upon which the calculation is based. From this the shorter but somewhat more complex method of calculation from a correlation table can be easily understood.

In the first column in Table XIX is the number given to each barley spike used to obtain both the determinations on weight of grain and percent of nitrogen. The weights of

seed in milligrams for the 25 entries used are put in the second column, headed x, and the corresponding determinations on the percent of nitrogen from the same individuals are given in the third column, headed y. The average of all the values of x and that of all the values of y are then found, and the deviations of each determination from the average are entered in the proper columns, headed d_x and d_y. The signs show whether the deviations are above or below the average. These deviations are then squared and entered in the last two columns, and from the sum of these squared deviations the standard deviations of x and y are found according to the formula already given.

Each deviation of x is then multiplied by the corresponding deviation of y and entered in the positive or negative column according to its sign. The algebraic sum of these products divided by the number which is obtained by multiplying the two standard deviations together and then by the total number of individuals, gives the Coefficient of Correlation. The formula is

$$r = \frac{\Sigma d_x \cdot d_y}{n \cdot \sigma_x \cdot \sigma_y}$$

Where r is the Coefficient of Correlation, the large Greek letter Σ represents the sum of a series of numbers, d the deviations from the mean, n the total number of individuals, and the small Greek letter σ the standard deviation.

Applying this formula in the problem given, $\Sigma d_x \cdot d_y = +12.628$.

$$\sigma_x = \sqrt{\frac{\Sigma d_x^2}{n}} = \sqrt{\frac{0.5966}{25}} = 0.154 \text{ percent}$$

and

$$\sigma_y = \sqrt{\frac{\Sigma d_y^2}{n}} = \sqrt{\frac{453.2060}{25}} = 4.258 \text{ mg.}$$

Therefore

$$r = \frac{+12.628}{25 \times 0.154 \times 4.258} = +0.770$$

The probable error of r is obtained from the formula

$$E_r = \frac{0.6745(1-r^2)}{\sqrt{n}}$$

The final answer is $r = +0.770 \pm 0.055$.

The Coefficient of Correlation ranges between the limits $+1$ and -1 and may be zero. A coefficient of .77 is comparatively high. Few quantitatively variable characters show as high a degree of correlation as this. Twenty-five is generally considered to be too small a number of individ-

TABLE XX

CALCULATING THE COEFFICIENT OF CORRELATION FROM THE CORRELATION TABLE BY THE SHORTENED METHOD, USING THE DATA GIVEN IN TABLE XVII

Weight seed y \ Percent Nitrogen x	1.2	1.4	1.6	1.8	2.0	f	d'	$f \cdot d'$	$f \cdot d'^2$	$\Sigma f \cdot d'x \cdot d'y$	
42.5		1				1	−2	−2	4	+2	−2(−1)
47.5	4	15	2			21	−1	−21	21	+23	−1[−8+(−15)]
52.5	5	49	25			79	0	0	0		
57.5		18	30	7		55	+1	+55	55	−11	+1(−18+7)
62.5			10	4	2	16	+2	+32	64	+16	+2(+4+4)
67.5				1		1	+3	+ 3	9	+ 3	+3(+1)
f	9	83	67	12	2	173		+67	153	+33	
d'	−2	−1	0	+1	+2						
$f \cdot d'$	−18	−83	0	+12	+ 4	− 85					
$f \cdot d'^2$	36	83	0	12	8	13					

Class interval $y = 5$. mg.

Correction, $y = 67 \div 173 = .387$

Mean, $y = 52.5 + (.387 \times 5) = 54.44$ mg.

Standard deviation $y = \sqrt{(153 \div 173) - .387^2} = .857 \times 5 = 4.29$ mg.

Class interval, $x = .2\%$

Correction, $x = -85 \div 173 = -.491$

Mean, $x = 1.6 + (-.491 \times .2) = 1.50\%$

Standard deviation, $x = \sqrt{(139 \div 173) - .491^2} = .750 \times .2 = .015\%$

Coefficient of correlation, r_{xy}

$$= \left[\frac{+33}{173} - (.387 \times -.491)\right] \times \frac{1}{.857 \times .750} = .593$$

uals from which to calculate a reliable coefficient. When calculated from the entire number, 173 individuals, the coefficient is $+0.593 \pm 0.033$. The correlation between kernel weight and oil content in oats is -0.447 ± 0.036.

The correlation table.—When large numbers are employed it is easier to arrange the data in a correlation table, as already shown, and to calculate the coefficient by multiplying the number of individuals in each square by their deviations from the means of each of the two characters in turn, as shown in Table XX. The means and standard deviations are calculated by the short method previously given. The only part of the process that needs explanation is the derivation of the column headed $\Sigma f d'_x d'_y$. The numbers given here are the sums of the frequencies multiplied by the deviations from both assumed means. For example, take the second horizontal row of frequencies in Table XX. Their deviation in weight of seed is -1 class. There are 4 which deviate -2, 15 deviate -1, and 2 deviate 0 classes from the assumed mean of percent nitrogen. Therefore $-1[-8+(-15)+0]=+23$. The values for all the horizontal rows are obtained in the same way and their algebraic sum is divided by the total number of entries in the table. From this is subtracted algebraically the product of the two corrections. The result is then divided by the product of the two standard deviations, stated in class intervals, to give the Coefficient of Correlation. The formula by the shortened method is

$$r_{xy} = \left(\frac{\Sigma f d'_x d'_y}{n} - c_x c_y \right) \left(\frac{1}{\sigma_x \sigma_y} \right)$$

Application of the correlation coefficient.—The usefulness of the Coefficient of Correlation is well shown by the results obtained by Blakeslee, Harris, and others, from data secured at the Storrs Station showing the association between pigmentation in certain parts of the body and egg production in hens. They have found that the amount of yellow in the ear lobes, beak, shanks, and other parts is negatively corre-

lated with the number of eggs that the hen has laid. Table XXI shows the amount of correlation between the degree

TABLE XXI

CORRELATION BETWEEN THE AMOUNT OF YELLOW PIGMENT IN THE EAR LOBES OF FOWLS IN OCTOBER AND EGG PRODUCTION FOR THE PREVIOUS MONTHS OF THE YEARS

Data from Blakeslee, Harris, Warner and Kirkpatrick, in Storrs, Connecticut A. E. S. Bull. 92

Month	1913–1914		1914–1915		Difference in Correlation 1913–1914, 1914–1915	Diff./E. Diff.
	Correlation	r/Er	Correlation	r/Er		
November...	$-.167 \pm .037$	4.51	$-.148 \pm .027$	5.48	$-.019 \pm .046$	0.41
December...	$-.271 \pm .036$	7.53	$-.230 \pm .033$	6.97	$-.041 \pm .049$	0.84
January.....	$-.229 \pm .036$	6.36	$-.228 \pm .033$	6.91	$-.001 \pm .049$	0.02
February....	$-.193 \pm .037$	5.22	$-.176 \pm .034$	5.18	$-.017 \pm .050$	0.34
March.....	$-.086 \pm .038$	2.26	$-.080 \pm .035$	2.29	$-.006 \pm .052$	0.12
April.....	$-.000 \pm .038$	0.00	$-.056 \pm .035$	1.60	$+.056 \pm .052$	1.08
May.....	$-.114 \pm .038$	3.00	$-.194 \pm .034$	5.71	$+.080 \pm .051$	1.57
June.....	$-.170 \pm .037$	4.60	$-.202 \pm .033$	6.12	$+.032 \pm .050$	0.64
July.....	$-.324 \pm .034$	9.53	$-.267 \pm .032$	8.34	$-.057 \pm .047$	1.21
August.....	$-.429 \pm .031$	13.84	$-.354 \pm .030$	11.80	$-.075 \pm .044$	1.70
September...	$-.663 \pm .022$	30.14	$-.663 \pm .020$	33.15	$+.000 \pm .030$	0.00
October.....	$-.761 \pm .016$	47.56	$-.751 \pm .015$	50.07	$-.010 \pm .022$	0.45

of yellow pigmentation of the ear lobes, as measured by a color top, in October, and egg production during each month of the preceding year. The data were obtained for two different years with White Leghorn hens and their egg records as obtained in the annual egg-laying contests. In every case a negative correlation was found, and the coefficients are significant for every month except March and April. These two months come during the season of most active laying, when hens which do not lay in the fall and winter are usually productive if they lay at all. The differences between the Coefficients of Correlation for the same months in the two years are none of them more than twice their probable errors, showing a remarkably close agreement between the two years' findings. Considerably more confidence can be given to these results, based upon ade-

quate numbers statistically treated, than to the casual observations of poultrymen concerning such a correlation.

A large number of correlations have been calculated for corn, comparing various ear characters with the yield of grain obtained from the plants grown from these ears, in the attempt to find some reliable guide by which to select high-producing seed ears. The figures obtained by Olson, Bull, and Hayes at the Minnesota Station, and by McCall and Wheeler at the Ohio Station, are given in Table XXII. In

TABLE XXII

CORRELATION BETWEEN EAR CHARACTERS AND YIELD IN CORN

Data from Olson, Bull and Hayes, in Minnesota A. E. S. Bull. 174 and McCall and Wheeler, in Jour. Agronomy

Character	Correlation	r/Er	Correlation	r/Er
Length	$+.098 \pm .040$	2.45	$+.102 \pm .651$	0.16
Weight	$+.047 \pm .044$	1.07	$+.087 \pm .066$	1.32
Circumference	$-.052 \pm .041$	1.27	$+.180 \pm .064$	2.81
Shelling percent	$+.157 \pm .043$	3.65		
Butts	$+.006 \pm .037$	0.16		
Tips	$+.030 \pm .038$	0.79		
Kernel uniformity	$+.048 \pm .037$	1.30		
Variety character	$+.033 \pm .037$	0.89		
Total score	$+.119 \pm .038$	3.13		

only a few cases are the coefficients large enough to be significant when compared with their probable errors, and in these instances the correlations are so low as to indicate very little value in selecting seed corn based upon the visible characters of the ears.

Causes of correlation.—From the illustrations given it will be seen that correlated variation may arise from different causes. The same influences which tend to develop an individual in one respect may also bring about a corresponding change in other characters. These influences may be environmental or hereditary, or they may be due to both, as is shown in the physiological relation between pigmenta-

tion and egg laying. Normally the yellow pigment is deposited in the yolks of the eggs; but if eggs are not laid in large numbers, the pigment accumulates in the body and shows in various places. The egg record, whether good or bad, is due both to the care and feed and to the hereditary constitution of the hen. The amount of pigment is merely an indicator of past performance and as such has value as a means of selecting for future egg-laying ability and for breeding purposes.

Other correlations may be due to the manifestation of the same hereditary factor or factors in different parts of the organism, as in color of stem and color of flowers. Correlalation may also result from the transmission of a combination of herditary factors. If a fruit fly with yellow body and white eyes is crossed with a gray-bodied fly with red eyes, the second generation will produce a large number of individuals with yellow bodies and white eyes or with gray bodies and red eyes. Very few will have the reverse combinations of yellow body and red eyes or gray body and white eyes. This results from the fact that these determiners for body and eye color are carried in the same chromosome and are closely linked. Correlations of this kind, where the linkage is loose, are not reliable, since crossing-over may occur at any time and in that event the association is abruptly reversed.

Classification of correlations.—In general, correlations may be classified as **somatic** and **germinal.** Somatic correlations result from external environmental influences which affect different parts of the organism in the same way, or they may be different expressions of the same growth processes working within the organism. Germinal correlations have their basis in the germplasm and are due either to different expressions of the same factor or factors or to different factors carried in the same chromosome and closely linked.

Correlation between parents and offspring.—The correlation coefficient has another important use in distinguishing

between variations which are purely environmental and those which are due to heredity. This distinction is brought out by the correlation between parents and offspring. If the deviations above the average which certain individuals show are due to heredity, the offspring should also tend to be above the average in this respect. This is illustrated by Johannsen in the average weight of seed of beans, given in Table XXIII. The correlation coefficient of $+0.336 \pm 0.008$,

TABLE XXIII

CORRELATION IN THE WEIGHTS OF BEANS BETWEEN THE SEED PLANTED AND THE CROP HARVESTED WHERE THE SEED PLANTS ARE NOT THE DIRECT DESCENDANTS OF A SINGLE INDIVIDUAL

Data from Johannsen

Weight Seed Planted	Weight Seed Harvested									
	10	20	30	40	50	60	70	80	90	
20		1	15	90	63	11				180
30		15	95	322	310	91	2			835
40	5	17	175	776	956	282	24	3		2238
50		4	57	305	521	196	51	4		1138
60		1	23	130	230	168	46	11		609
70			5	53	175	180	64	15	2	494
	5	38	370	1676	2255	928	187	33	2	5494

$r = +.336 \pm .008$

between parent and offspring, indicates that those plants which produce large seeds tend to give plants with seeds somewhat heavier than the average. In this case the mother plants were grown from a mixed lot of seed of one variety. When the same determination was made for plants that were all descended from a single individual, data for which are shown in Table XXIV, Johannsen found that there was no significant correlation ($r = -.018 \pm .025$) between parent and offspring.

In the first case he concluded that the variation in seed

TABLE XXIV

CORRELATION IN WEIGHT OF BEANS BETWEEN THE SEED PLANTED AND THE CROP HARVESTED WHERE THE SEED PLANTS ARE THE DIRECT DESCENDANTS OF A SINGLE INDIVIDUAL

Data from Johannsen

Weight Seed Planted	Weight Seed Harvested										
	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	
27.5			1	5	6	11	4	8	5		40
32.5				1	3	7	16	13	12	1	53
37.5		1	2	6	27	43	45	27	11	2	164
42.5	1		1	7	25	45	46	22	8		155
47.5			5	9	18	28	19	21	3		103
52.5		1	4	3	8	22	23	32	6	3	102
57.5			1	7	17	16	26	17	8	3	95
	1	2	14	38	104	172	179	140	53	9	712

$r = -.018 \pm .025$

weight was partly due to heredity. In the second case he assumed that all the plants were alike in hereditary constitution, and that the variations were due wholly to environmental modifications. In the one case it would be possible to increase the average weight of seed by proper selection. In the other, selection would be wholly without effect. This important difference between the two lots of plants will be more fully dealt with in the following chapter.

CHAPTER IX

THE COMPOSITION OF PLANT AND ANIMAL POPULATIONS

INDIVIDUALS having exceptional qualities commonly fail to pass on these qualities, in the same high degree of development, to all of their immediate offspring. The prize-winning animals at the livestock expositions are not always the parents of succeeding winners. The finest specimens of plants at the fairs are often no better for seed purposes than other individuals which are not so excellent in appearance. Similarly, the very poorest individuals, although they are seldom used for propagation, often give offspring that are much better than they themselves are.

Galton's investigation of human stature.—This tendency on the part of the progeny to return to the common level of the stock to which the extreme parents belong was first considered by Sir Francis Galton. Human stature was chosen as the character to be studied. Galton compared 204 English parents with their 928 adult offspring. After multiplying each female height by 1.08, to correct for the average amount by which the male exceeds the female in stature, the midparental height was calculated for each pair of parents. In the material worked with, this average height of parents was found to range from 64 to 73 inches. All the parental pairs were put into nine classes differing by one inch in height. The average of the adult children for each of these classes is shown graphically in Fig. 92. In general, the offspring of the parents above the average are shorter than their parents, while the parents below the average have children who are taller than their parents,

and parents of average height have children of about average height.

Regression.—Galton calculated the amount of deviation of each class of parents and of their offspring from the mean of the whole group, and found that the offspring differed from the general average only about two-thirds as

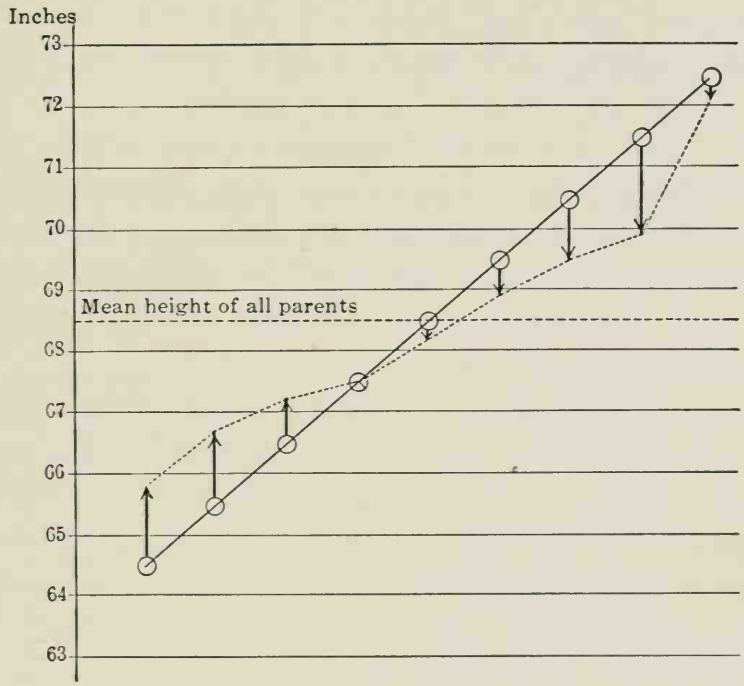


FIG. 92.—Diagram illustrating Galton's law of regression. The circles represent the height class to which the parents belong, while the arrow-points indicate the average height of their respective offspring. The children of short parents are taller, and those of tall parents shorter, on the average, than their respective parents. (From Walter, based on data by Galton in "Genetics," courtesy of Macmillan Co.)

much as the parents differed. From these results, which were substantiated by findings based on other characters and in other organisms, Galton formulated his **Law of Regression,** or the tendency of succeeding generations to revert toward mediocrity. This law is generally stated as follows:

Average parents tend to produce average offspring; parents below the average tend to produce offspring below

the average; parents above the average tend to produce offspring above the average; *but the progeny of extreme parents, whether above or below the average, inherit the parental characters in a less marked degree than the latter were manifested in the parents themselves.*

Regression applies only to groups.—It is obvious that this law of regression applies only to the average of large numbers and can not hold for particular individuals; otherwise extreme individuals would never be produced. Regression is also shown by the parents as well as the offspring. The parents of exceptional individuals tend to be nearer the general average than their offspring, and the regression is the same in amount as in the reverse case. In neither case can the regression be definitely predicted as any exact amount, as it varies with different characters and in different organisms.

Johannsen's investigations with self-fertilized plants.—Galton's observations were upon bisexual organisms, in which the variation was very largely due to differences in hereditary constitution. The Danish botanist, Johannsen, was the first to study variation in a self-fertilized organism, in which the germinal variation is largely eliminated and the differences therefore arise mostly from environmental modifications. For his investigations Johannsen chose the common garden bean. From a general lot of seed of the variety known as the Princess bean, he selected a number of the heaviest seeds, all weighing the same, 80 centigrams. Each plant grown from these seeds produced seeds which varied in size on the same plant, as would be expected, according to the number of seeds in the pod, the position of the pods on the plant, and the time the flowers appeared. The average weight of seed for each individual plant also differed and ranged from 35 to 60 cg. The seed of no plants averaged as heavy as the large seeds planted, although some individual progeny seeds were as large as the parental seed. The progenies as a whole showed regression, but individual seeds varied widely.

Effect of selection upon seed weight.—Johannsen next endeavored to change the average seed size by selecting the largest and smallest seeds from the crop grown on one plant. Somewhat to his surprise, he found that the heaviest seeds gave progenies which averaged no more in seed weight than the progeny from the smallest seeds. All of the descendants of a single plant Johannsen called a line. Selection of extremes in a number of different lines was continued for six generations, with the result shown in Table XXV for

TABLE XXV

THE RESULT OF SELECTING THE SMALLEST AND LARGEST SEEDS FOR PLANTING DURING SIX SUCCESSIVE GENERATIONS IN TWO LINES OF BEANS DESCENDED FROM ONE PLANT

Data from Johannsen

Generation	Average Weight of Selected Parent Seed		Difference	Average Weight of Offspring		Difference
	Minus	Plus		From Minus Parent	From Plus Parent	
1	60	70	+10	63	65	+2
2	55	80	+25	75	71	−4
3	50	87	+37	55	57	+2
4	43	73	+30	64	64	0
5	46	84	+38	74	73	−1
6	56	81	+25	69	68	−1

one of these lines, which is typical of the behavior of all the selected lines. This is illustrated diagrammatically in Fig. 94.

A pure line.—In the last generation of selection, the lightest seeds, weighing on the average 56 cg., gave an average progeny weighing 69 cg., while the heaviest seeds, weighing on the average 81 cg., produced in their progeny practically the same average weight as did the lightest beans, that is, 68 cg. Both the parents and their progenies

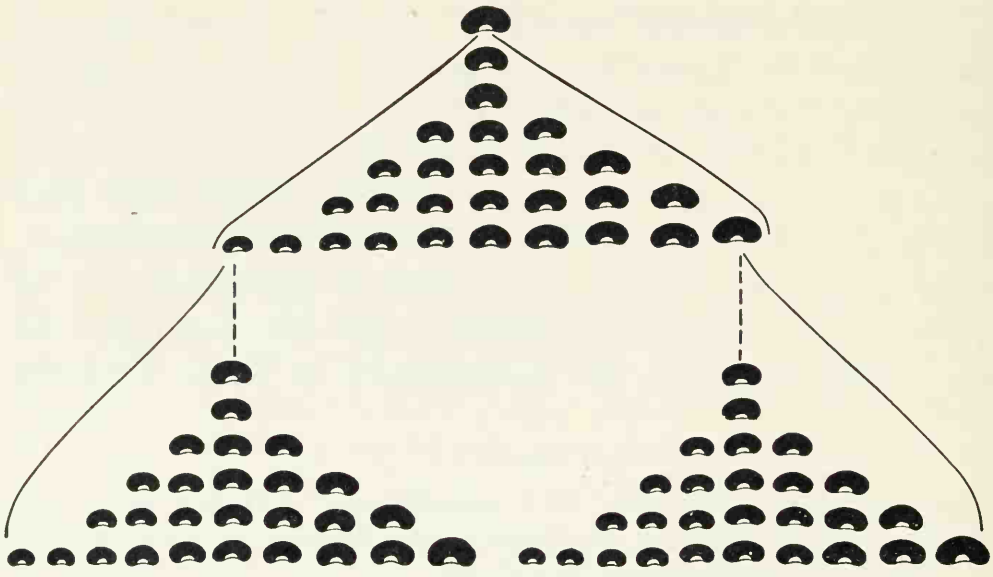


FIG. 93.—The result of selecting for seed the largest and smallest beans grown on one plant. Above is the frequency distribution of the seeds from the mother plant. Below are the results obtained in the two progenies, showing that environmental variations are not transmitted. (After Baur in "Grundlagen der Pflanzenzüchtung," courtesy of Gebrüder Borntraeger.)

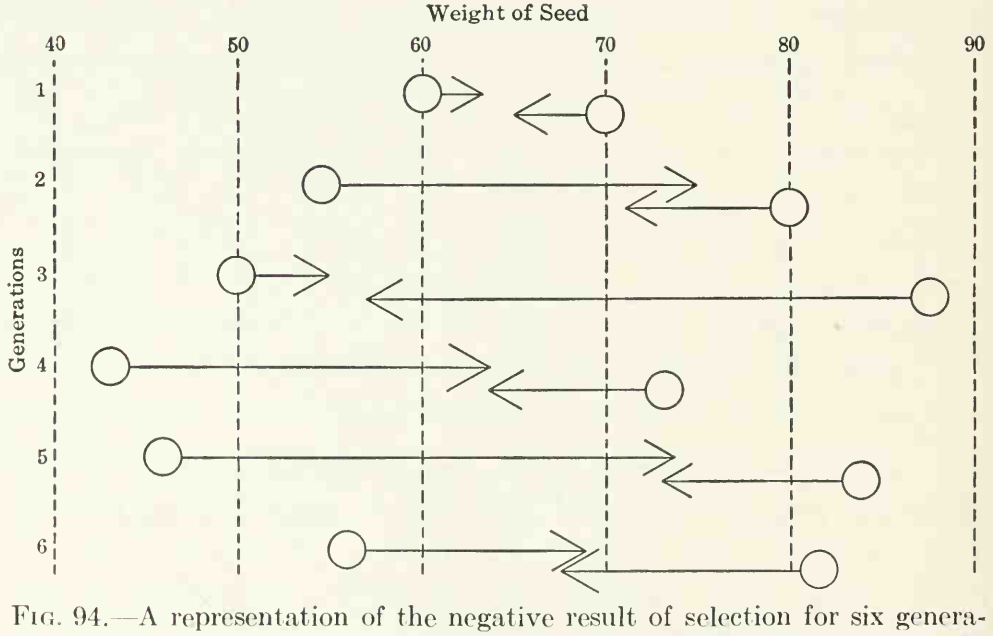


FIG. 94.—A representation of the negative result of selection for six generations in two lines descending from one plant. The circles indicate the average seed weight of the selected parents and the arrow-points their respective progeny. While the plus and minus selected parents differ greatly in each generation, the averages of the two progenies are alike within the limits of random sampling. (After Walter, based on data from Johannsen in "Genetics," courtesy of Macmillan Co.)

varied in weight from year to year, owing to seasonal conditions. Thus, in the third generation there was a poor year for seed weight and in the fifth a good year, but it should be noticed that both the minus and plus selections varied in this way about equally. After six years of selection of the heaviest and lightest seeds, there was no difference in the descendants of a single plant. Johannsen therefore concluded that the common fluctuating variations due to the environment in which the plant grows have no influence upon the following generations in the case of seed weight of beans, and that therefore all the descendants of a single self-fertilized plant are alike in their hereditary constitution, and that environmental variations are not carried over from one generation to the next. The descendants of such a single homozygous organism, propagated exclusively by self-fertilization, Johannsen called a **pure line.**

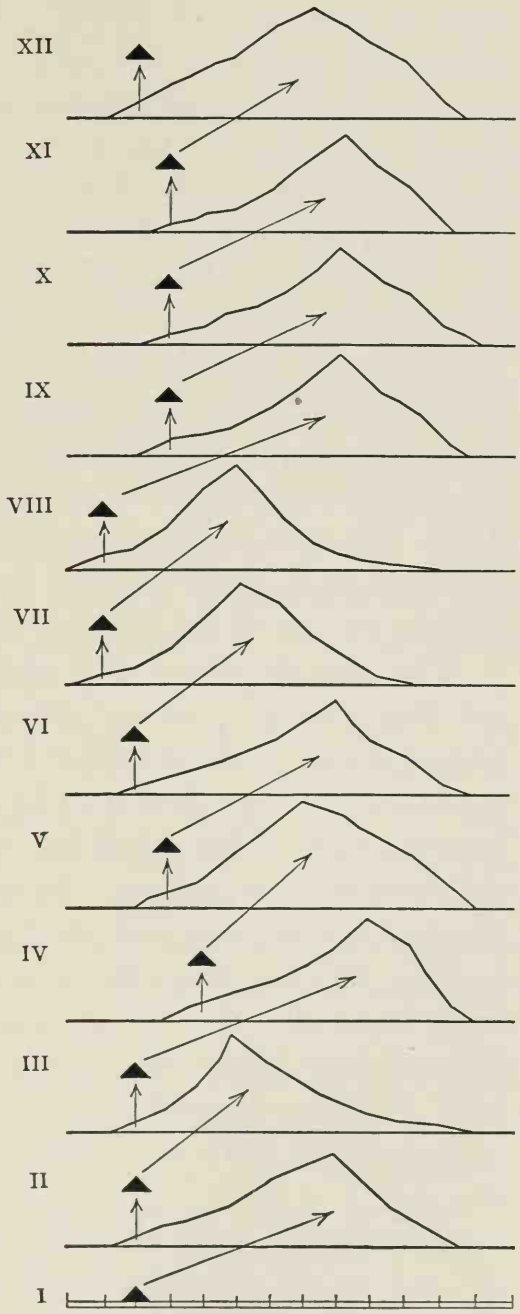


FIG. 95.—A representation of the result of selection during twelve generations within a strain of the Colorado potato-beetle. (After Tower, from Walter in "Genetics," courtesy, Macmillan Co.)

Tower's experiment with the potato beetle.—A similar selection experiment with a bisexually reproducing animal,

the Colorado potato beetle (*Leptinotarsa decimlineata*) has been carried out by Tower. These insects vary in color. Extremely dark-colored individuals from a single family were selected for mating, and this procedure was continued for twelve generations, with the result shown in Fig. 95. At the bottom of the figure is a graded scale representing the range in color. The dark triangle shows the position on this scale of the progenitors selected to produce the following generation. The frequency curves give the distribution in color of each successive progeny, the arrow head showing the average position. In spite of the fact that extreme individuals were selected in each generation, the progeny swung back to the general position of the family. As in the case of seed weight in beans, some fluctuation occurred from generation to generation, but no progressive change was made during the entire experiment.

The specifications of a pure line.—It is therfore apparent that a pure line is not dependent upon any one mode of propagation. The important consideration is that all the members of a pure line be alike in respect to their hereditary constitution. This condition is most generally met with in self-fertilized organisms, because this process tends to eliminate automatically all heterozygous combinations of factors, leaving only like combinations. After hybridization, however, the homozygous descendants differ in the factors they carry, so that a pure line is usually found only in the descendants of a single homozygous individual, which have not themselves undergone any germinal change.

A pure line may also exist in cross-fertilized organisms as long as all the individuals are germinally exactly alike. This occurs generally only after long-continued close inbreeding. This condition is practically never found in domesticated animals and plants, because the mixing of different types is such a common practice that absolute uniformity in hereditary constitution is nearly impossible. But many cross-fertilized wild species are uniform and

very closely approach the condition of a pure line. Moreover, when similar organisms which are identical in their germinal determiners with regard to particular characters interbreed, their progeny will constitute a pure line *as far as this particular character is concerned.* With the potato beetles selected by Tower, the members of the family were alike with respect to color factors although they may have differed genetically in other characters.

In parthenogenetic reproduction, where no reduction in chromosome number takes place, and there is no fertilization by the male germ cell, the descendants of a single individual are usually exactly alike in germinal constitution and fulfill all the conditions of a pure line. Similarly, vegetative propagation does not permit recombination to take place, and all the descendants of one individual propagated exclusively without seeds, called a **clone,** correspond to a pure line whether they are heterozygous or homozygous.

The permanence and definition of a pure line.—The continuation of a pure line in any form of propagation is dependent upon the non-occurrence of any germinal change, whether due to Mendelian recombination, chromosome aberrations, or factor mutations. A pure line must therefore be defined as *the descendants of one or more individuals of like germinal constitution, which have not undergone any germinal change.*

Plant and animal populations.—A variety of plants or animals is usually composed of more than one pure line. These are variously called elementary species, subvarieties, or biotypes. On account of the crossing which does occur occasionally, even in organisms that are largely self-fertilized, and the consequent Mendelian recombination, also on account of changes which take place in the individual factors themselves, and irregular distribution of chromosomes, most varieties contain a large number of pure lines. Any aggregation of individuals, however similar or diverse they may be, is called technically a **population.** A field of wheat or of corn is a population. A herd of cattle or a drove of

swine is a population. A population is therefore made up of one or more pure lines.

Classification of living organisms.—All forms of life, domesticated as well as wild, are classified into species. A species is a more or less arbitrary group of individuals having certain features in common and distinguished from all other forms by some important characters or properties. The members of one species are generally fertile among themselves but sterile with members of other species. There are many exceptions to this rule. Species of domesticated animals and plants are further subdivided into breeds and varieties. Breeds of similar type may be grouped together, as the beef and dairy types of cattle, wool and mutton types of sheep, or meat and egg breeds of poultry. This classification is largely based on utility and it distinguishes well-marked hereditary differences. With plants, there are flint and dent types of corn, winter and spring varieties of wheat. Within the variety, or breed, certain characteristics may differentiate some families from all the others, and these are called strains. Not all kinds of Reid's Yellow Dent corn are alike. Some may be consistently earlier in maturity or differ in size and shape of ear sufficiently to be recognized. In the same way, animal families are distinguished by well-marked characteristics. But variation does not stop there. Every plant or animal has its individual features which make it different from every other. These differences may be very small, and not readily apparent when they are found in minor details.

The power of selection.—As a consequence of the widespread acceptance of the Darwinian theory of evolution, it is generally believed that the selection of these individual differences brings about a continual progressive alteration in any desired direction. Domesticated animals and cultivated plants have been enormously changed from their nearest wild relatives. This has been brought about by selecting the best plants for seed and the most desirable animals for mating. Experience, therefore, seems to bear

out the contention that selection is an agency in producing changes.

The operation of selection.—How selection may bring about a change was first clearly demonstrated by Johannsen. It was stated at the beginning of this chapter that a number of seeds of the Princess bean, all weighing the same, gave plants which averaged quite differently. Each seed, therefore, presumably belonged to a different pure line. Johannsen weighed separately all the beans grown in one year in several lines which were the descendants of single plants in each case. Each was found to give the usual frequency distribution in seed weight and the results are shown graphically in Fig. 96. In this illustration all the seeds in each tube weigh the same and the tubes in the different pure lines containing the same class of seeds are placed directly above each other. At the bottom all the lines are combined, seeds of the same weight class being put together. Such a combination of pure lines represents a population and is typical of the variety from which the several lines were taken. The distribution of the seeds in

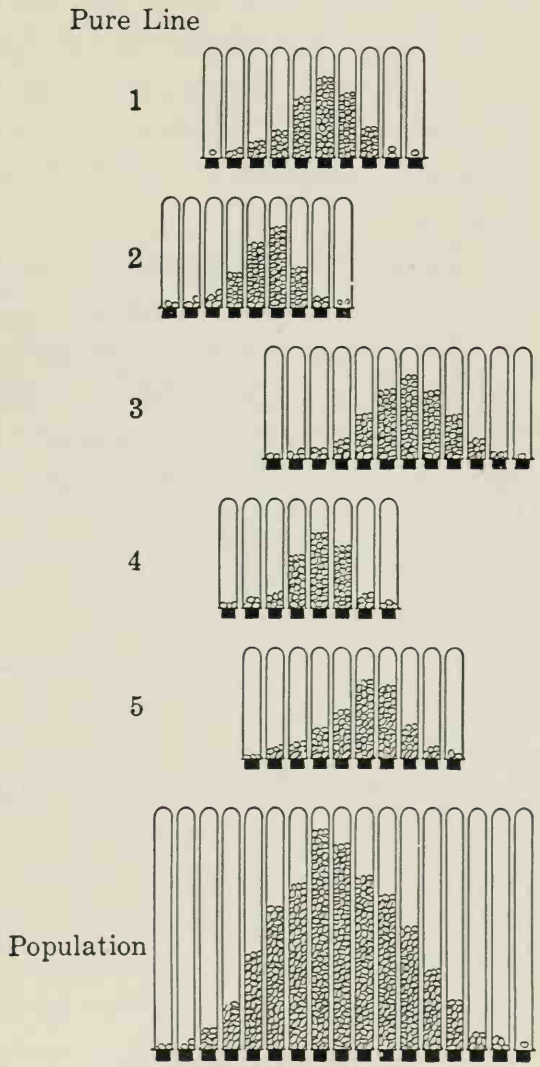


FIG. 96.—The frequency distributions of five pure lines of beans and the population formed when all are put together. (After Johannsen, from Walter in "Genetics," courtesy of Macmillan Co.)

the general population is quite similar to their distribution in the several lines. There is an intergrading in weight from the smallest to the largest.

By examining each line separately it will be seen that an extreme size of seed in one line, such as the smallest seeds in No. 3, may be the most frequent size in another line, as in No. 2. But when all are combined there is no way of telling by inspection to which pure line the individual seeds belong.

In the combined population, all the seeds in one tube are alike with respect to weight. They will give different results in the next generation, according to the pure line to which they belong. On the other hand, the seeds of any one pure line fall into different weight classes but all will give the same result in the next generation irrespective of their size. To such individuals, which may differ in appearance but breed alike, Johannsen gave the term **genotype.** All individuals that look alike but may breed differently he considered as belonging to one **phenotype.** Genotypes are classified according to their germinal constitution. Phenotypes are classified according to their somatic appearance.

Selection directed towards genotypes.—Selection in the past has largely been confined to phenotypical differences. It is obvious that this process has been successful only in so far as it also sorted out different genotypes. In the case of seed weight in beans, just given, if it were desired to increase the weight of seed, selection of the heaviest 25 percent of the seeds from this population would probably eliminate all of the pure lines except Nos. 1, 3, and 5. The next generation would contain a large number of plants of line No. 3 and a few of Nos. 1 and 5. While the crop grown from these selected seeds would not all be as heavy as the seed planted, there would be an appreciable gain in average weight on account of the complete elimination of the light lines, Nos. 2 and 4. Further selection would in time eliminate lines 1 and 5, and thus there would be a continued response to selection as is usually the case when attention is given to

forms that have not been extensively selected. After all but one of the lines were eliminated, further selection would bring about no change, and the limit of selection in this material would then be reached. Any further change would have to await a germinal mutation or cross-fertilization with plants of another line.

If the selection were made more rigid at the start, and only a few of the very heaviest seeds were chosen for plant-

FIG. 97.—Differences in clover plants from the same field. Until their progenies are grown and compared, no one can tell whether the difference is genotypical or phenotypical.

ing, then all of the lines except No. 3 would be eliminated at the start. In this way a more pronounced response to selection would be obtained but further selection would be without results.

Difficulty of isolating desirable genotypes.—In this illustration the problem is presented in the simplest form possible. In actual practice there are usually a much larger number of pure lines to deal with. The characters with which selection is most commonly concerned are pro-

ductiveness, hardiness, quality, and similar features that are dependent in some measure upon all parts of the organism and are governed by a large number of factors. Many of the best individuals, in respect to their development of desired qualities, are equally fine but belong to pure lines which fluctuate about different modes. In fact, the best genotypes may have no representatives in the extreme

FIG. 98.—The descendants of two tobacco plants selected for resistance to root-rot and grown on infected soil. The original variety from which they were selected is shown in the center. The two selections are on either side. (After Valleau in Kentucky A. E. S. Cir. 28.)

upper classes of phenotypes, and therefore mass selection either fails to secure them at all, or if it does secure them they are mixed with a number of other less desirable genotypes. Obviously, the best procedure with self-fertilized plants is to isolate single individuals, compare their progenies, select the best of these, and propagate single genotypes. On account of soil and seasonal variations, it is necessary to test different lines during several years in order to determine accurately their relative value.

Mass selection *versus* pure line selection.—When a number of individuals whose ancestors are unknown are chosen for propagation, this process is called **mass selection.** While it is true that many individuals in a mixed population belong to the same pure line, the only certain way of obtaining a pure line in self-fertilized plants is to propagate from single individuals. In spite of the handicap of a limited seed supply in most plants, the advantages gained in dealing with a fixed type, which will not vary in the way a mixed type will, far outweigh the delay necessary to increase individual plants until satisfactory numbers are obtained.

Selection a sorting-out process.—Selection in self-fertilized, homozygous organisms is thus merely a sorting-out process, similar to that by which the farmer separates the different kinds of grain from a mixed field of wheat, oats, and barley. There is, however, this important difference: the different pure lines within a variety can seldom be separated by inspection.

Pure lines in cross-fertilized organisms.—The pure line concept is equally applicable to cross-fertilized organisms but there the matter is far more complex. In addition to the environmental fluctuations there is the enormous variability due to Mendelian recombination. In heterozygous material pure lines do not exist as such. All that selection can do is to sort out a group of individuals which approach more or less closely the condition of a pure line. Since most cross-fertilized animals and plants, and particularly domesticated forms, are dependent upon the continuation of interbreeding to maintain vigor, it is ordinarily impossible to reduce them to homozygosity in more than a relatively few characters which are not associated with vigor. Pure lines in color or in minor external features are easily established and will remain true to type without further attention, but in most cases any change from the average condition brought about by the isolation of superior individuals must be maintained by continued selection in the same direction. In this way it is possible to make great changes

on account of the great number of heterozygous genotypes from which one may draw. In cross-fertilized plants it is comparatively easy to alter the time of flowering and maturing. Size and form of plant and fruit are also modifiable within limits. Animals are quickly changed in coloring when differences exist in the stock worked with. Size, form, and time of maturing are also plastic. In other words, cross-fertilized animals and plants can be adapted to particular places and for special purposes more easily, as a rule, than self-fertilized plants. But when this adaptation is made, it is difficult to make any additional increase in productiveness.

Importance of progeny performance test.—With heterozygous as with homozygous material, selection is effective only in so far as it isolates genotypical differences. These are found not from the appearance of the individuals themselves, but in the behavior and development of their progenies. The basing of selection of the parents on the performance of their progeny, and not upon their own appearance, is therefore a fundamental principle in plant and animal improvement.

The pure line method applied to self-fertilized plants.—The most notable example of the application of this principle to plants is to be found in the new variety of winter wheat known as Kanred, produced by the Kansas Experiment Station and now being grown on more than 2,000,000 acres. Every plant on this vast area is directly descended from one single seed planted less than fifteen years ago. The long-staple variety of cotton, known as Pima, originated by this method by the United States Department of Agriculture, for the irrigated districts of the Southwest, now produces over 100,000 bales annually, and all plants trace back directly to a single plant selection.

Unit of selection.—It is, of course, clearly understood that the unit of selection in plants is the individual and not different parts. The saving of particularly fine fruits or seeds is sometimes advocated. For instance, with tomatoes,

the first fruit to set in a cluster is usually larger and finer than the others and is the first to mature. Some seedsmen take seed from such fruits and advertise this as an élite strain. As far as earliness is concerned, it makes no difference in the progeny whether the seed comes from the first or the last fruit to ripen, as long as the seeds are equally well developed and equally mature. If there is any difference, the last fruits to ripen will give the earliest plants. As was noted before, the New York Station demonstrated that immature tomato seed gives earlier ripening plants, but this is a transitory environmental effect and is not due to any germinal change. For the most part, seeds of large or small fruits are about equally well developed and are potentially alike in reproductive qualities. Practices such as these with tomatoes, or with beans in saving the largest seeds in the pod or from pods with greatest number of seeds are almost wholly wasted effort. Whatever result is obtained can be attributed to a carry-over effect due to a larger store of energy in the seed, and any differences obtained are usually negligible. Many plants store such large quantities of food in their seeds that ordinary differences in size have no material effect upon the seedlings.

It is also sometimes feared that the common practice of discarding the tip and butt seeds when preparing corn for planting may result in a tendency to produce ears which are less well developed at the butt and tip. A moment's reflection will show the absurdity of such a belief. If the cattle breeder selected only second-born calves and mated them at the proper time with other animals which were second in order of appearance, would he expect to produce in time a race in which only second-born calves resulted? Such a proposition is no more ridiculous than the previous one. As long as corn produces seeds, some will have to be placed at the tip and butt as well as the middle of the ear.

Such misunderstandings arise from a failure to appreciate the fact that characters, as such, are never inherited. As was brought out in Chapter II, it is only the potentiality

to develop into a particular condition in a definite environment that is passed on. The position of the seed on the plant is as much a part of the environment as is the soil or season in which it grows, and the ordinary modifications induced by the surroundings are not inherited.

Permanence of pure lines.—Since the permanence of a pure line depends upon freedom from factor mutations, irregular chromosome behavior in cell division, and outcrossing, and since these are known to occur at more or less infrequent intervals, some selection is needed in practically all forms to keep a variety true to type and up to its proper standard. With these precautions, pure lines in plants that are largely self-fertilized are actually quite constant. Louis de Vilmorin, of the seed firm of Vilmorin, in France, propagated four different varieties of wheat from single plants. Each year the best plants were chosen, and after fifty generations of selection representative heads were compared with specimens saved from the original lots. The similarity in size and form showed that no appreciable alteration had taken place in this long time. Neither was there any increase in yield. Although in this case selection may have tended to preserve the type rather than alter it, there was no noticeable change in the relative time of ripening, a character that is greatly influenced by the environment.

Stability of unit factors.—Since Mendel's work became known, it has been fully appreciated that a large part of the response to selection in a heterogeneous stock is due to a segregation and recombination of different germinal factors. In addition to this opportunity for alteration, it has been believed by many that the unit factors themselves vary in sufficient amount to furnish a means of inducing a change in any definite direction. Factors do vary, as has been abundantly proved. The controversy has to do with the amount and frequency of such changes. The experimental evidence goes to show that actual germinal changes, or mutations, are so infrequent that for practical purposes

this is a relatively unimportant factor in progressive variation.

Selection with hooded rats.—A selection experiment which for a long time has seemed to give some support to the contention that unit characters are progressively variable has been carried out by Castle with hooded rats. This type of rodent has the head and shoulders covered with a pigmented hood pattern which sometimes extends in a narrow strip down the middle of the back. The hooded pattern is recessive to the entirely pigmented condition. The recessive segregates breed true for the pattern when

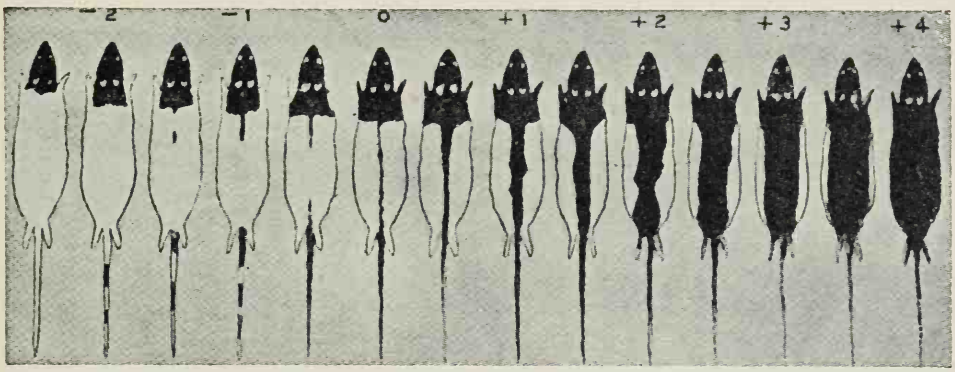


FIG. 99.—Diagram showing the range in variation of the hooded pattern in rats obtained by selection. (After Castle in Carnegie Institution Publication 241.)

mated among themselves, but the area of the skin which is colored is variable. From a small colony of such rats derived from less than a dozen individuals, the most pigmented and the least pigmented animals were chosen and mated among themselves. In this way two divergent lines were started. The progeny of the first selected line tended to be more pigmented than the progeny of the oppositely selected line. This difference steadily increased until, after seventeen successive generations, the minus line had no color on their backs, while in the other line after sixteen generations the members were almost entirely pigmented.

A notable effect has been brought about by selection along this line through a period of years. Castle formerly

contended that this change took place in the single hooded-pattern factor and that a progressive alteration might go on in either direction until completely colored or uncolored animals were obtained. Others have argued that the results are more probably due to modifying factors which have been sorted out by the selection process. It is held that one main factor controls the difference between hooded and self-colored patterns, while other minor factors modify the extent of pigmentation. That the latter view is the more reasonable Castle has recently conceded as the result of a critical test which he applied. The extreme types of both lines were crossed with a uniform wild race. The extracted recessives were again out-crossed to the same wild race, this being repeated three times. The outcome was that the plus and minus hooded patterns were reduced to practically the same grade in extent of area colored. The results of sixteen generations of selection were thus done away with by three crossings. If the difference in degree of pigmentation in the selected lines had been due to a change in a single factor extending over so many generations, it would be difficult to see how this could be reversed in three generations. On the hypothesis of modifying factors, crossing removed these and the main hooded-pattern factor was brought to the state where it was at the start.

In Drosophila, several modifying factors which intensify or dilute eye color have been found. These factors have been located in the chromosomes and their relations with other factors determined. Many variable characters which respond to selection in Drosophila, such as the number of bristles on the thorax and the number of facets in the compound eye, have been definitely shown to be due to the influence of numerous factors; and when complete homozygosity of all these factors is brought about, variability is reduced and selection is unable to make further change.

Selection experiments with corn.—Another well-known case whereby characters are altered continuously in a definite direction is supplied by the work of the Illinois Experiment

Station on corn. Starting with a common field variety, the plant breeders have selected for several different contrasted characters, such as plants with high and with low ears, and plants with erect and with declining ears. The method has been to select, in open-pollinated fields, plants which deviated the most in the direction sought for. Seed of these plants were grown in separated plots and again selected. After several years very great changes were brought about, as shown in Fig. 100 and Table XXVI.

Changing chemical composition by selection.—One of

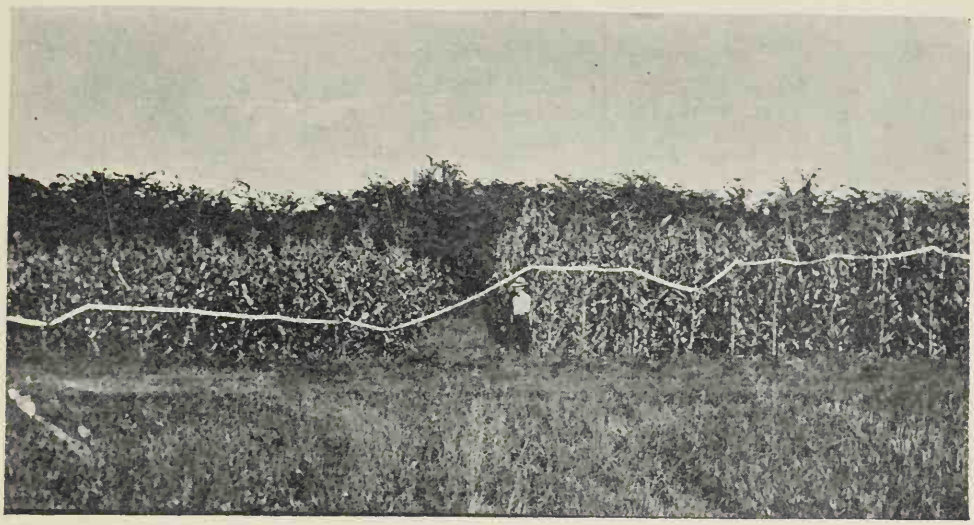


FIG. 100.—Result of six years' selection for high and low ears in corn. The white tape shows the position of the ear of the first plant in each row. (After Smith in Illinois A. E. S. Bull. 132.)

the first definitely planned and carefully executed experiments on plant breeding was begun by Hopkins at Illinois, in 1896, and aimed to alter the composition of corn in respect to certain ingredients. The work has since been carried on by L. H. Smith. Starting with 163 ears of a variety known as Burr's White, chemical analyses were made of a few grains from each ear, and the ears were then separated into four lots on the basis of high and low percent of protein and high and low percent of oil. Each lot was grown separately. A large number of ears of the crop harvested were again analyzed, and seed selected from the extreme

TABLE XXVI

AVERAGE DIFFERENCES IN THE CROP OF CORN SELECTED FOR HIGH AND FOR LOW EARS DURING SIX SUCCESSIVE GENERATIONS

Data from Smith, in Illinois A. E. S. Bull. 132

Generation	Height of Ear			Number of Internodes below Ear		
	High-ear Plot	Low-ear Plot	Difference	High-ear Plot	Low-ear Plot	Difference
1	56	43	13	9	7	2
2	50	38	12	8	6	2
3	63	42	21	8	7	1
4	57	26	31	9	6	3
5	72	33	39	9	6	3
6	57	23	34	8	5	3
	Height of Plant			Total Number of Internodes on Stalk		
1	114	103	11	15	14	1
2	106	97	9	15	13	2
3	128	107	21	15	14	1
4	116	86	30	15	11	4
5	130	100	30	16	13	3
6	114	79	35	16	12	4

deviations. After the work had been carried along in this way for nine years, it was necessary to change the plan of the experiment somewhat, as the close selection tended to increase the number of related individuals, and the consequent inbreeding resulted in reduced vigor and lessened yield. Accordingly, from then on about 24 ears were selected in each line, one row planted from each ear, and alternate rows detasseled. The selections were made from the detasseled rows.

Although there has been considerable seasonal fluctuation in composition, there has been a steadily widening difference in percent in the two oppositely selected lines in

each case, as shown in Figs. 101 and 102, where the data are given in the form of curves. From an average of 10.92 percent in the original corn, the protein has been increased

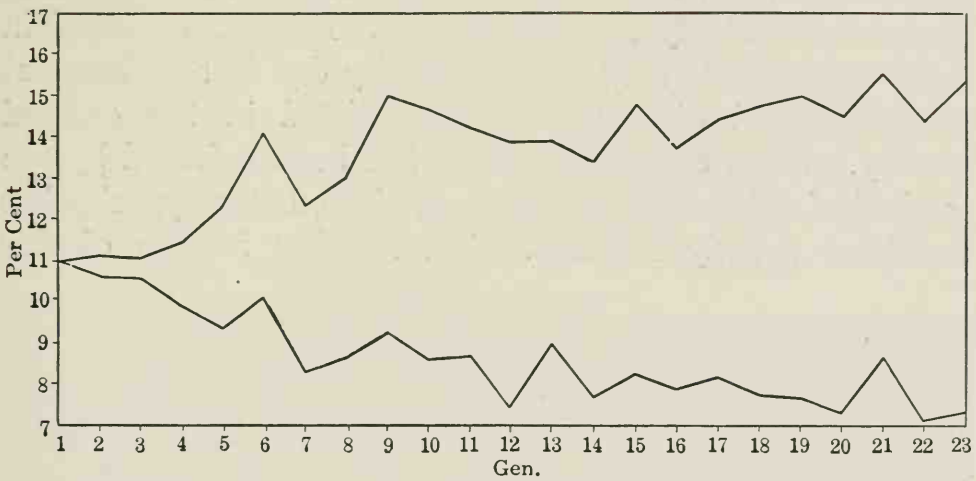


FIG. 101.—Graphical representation of the results obtained at the Illinois Experiment Station in selecting corn for high-protein and for low-protein content. (After East and Jones in "Genetics.")

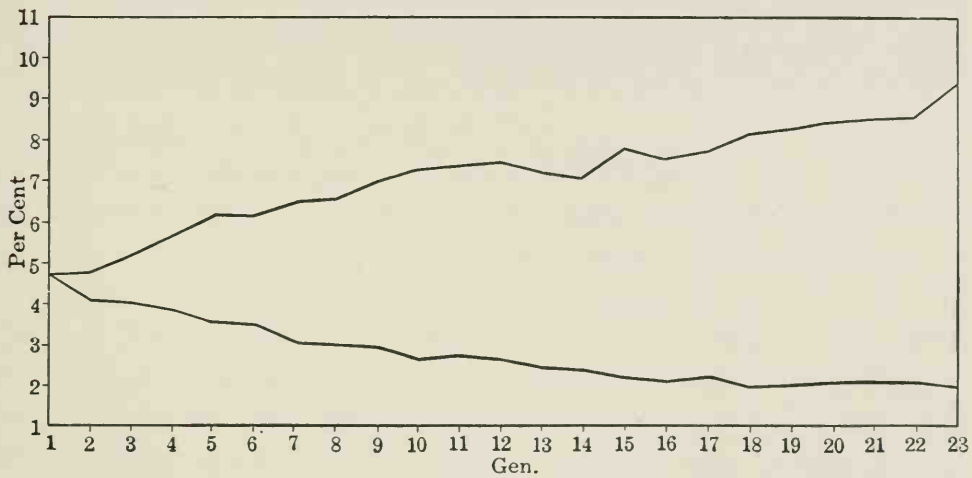


FIG. 102.—Graphical representation of the results obtained at the Illinois Experiment Station in selecting corn for high-oil and for low-oil content. (After East and Jones in "Genetics.")

to 14.53 percent and reduced to 7.74. Similarly, oil content has been brought to 8.46 percent in the plus selected line, and 2.03 percent in the reverse direction.

An examination of the curves shows that the greatest change was made in the first ten generations of selection.

In later generations the amount of difference has not increased so rapidly, although there has been an appreciable advance in the direction of selection. Bearing in mind the conclusions from other selection experiments and the fact that corn is widely cross-fertilized, the results obtained in these experiments are probably wholly due to a sorting out of genotypical differences which existed in the original variety. Since cross-fertilization has been enforced by the method of detasseling to maintain vigor, heterozygosity has not been greatly reduced. One striking feature of this

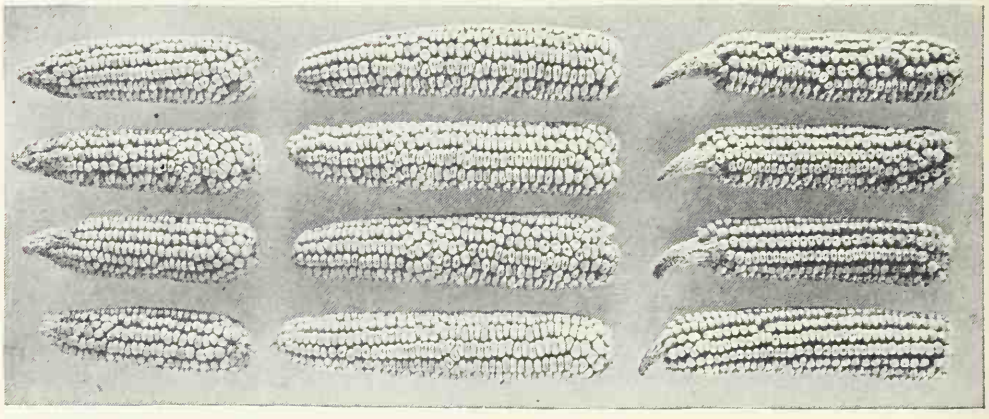


FIG. 103.—Three strains of Illinois high- and low-protein corn, further selected in self-fertilized lines. The low-protein strain in the center averages from 7 to 8 per cent while the two high-protein strains on either side average from 16 to 19 percent.

selection experiment lends support to this interpretation. A pedigree record of the ears selected in each generation has been kept, and an examination of this, as pointed out by Surface, shows that in the high protein line all the selections after the ninth generation trace back to one original ear at the start. Similarly in the low protein, only 2 of the 12 original lines survived. In the high oil, only 3 out of 24, and in the low oil 2 out of 12 are represented after the eleventh generation.

In this naturally widely cross-fertilized species, selection has a great opportunity to produce an effect due to the amount of heterogeneity in genetical composition. The

fact that selection, as it is usually practiced with corn, takes into consideration the qualities of only the seed parent and not of the pollen parent, further complicates matters. Selection may, therefore, produce some change for an indefinite period, as heterozygosity can hardly be entirely eliminated in a continually cross-fertilized organism. But the final result is limited by the hereditary constitution of material at the start; and when the most favorable combination of factors has been brought about, no further progress can be made unless other material is added or germinal changes in the right direction occur.

Selection in self-fertilized lines.—When selection for differences in chemical composition is carried on with self-fertilized corn plants, as shown by East and Jones at the Connecticut Station and Hayes at the Minnesota Station, the change is more rapid; and when homozygosity is reached, the composition which has been attained can be maintained without further selection. Since self-fertilization, accompanied by selection, automatically sorts out genotypical differences more effectively than any system of selection in continually cross-fertilized material, it seems evident that the Illinois results are to be interpreted on the basis of segregation and recombination, rather than progressive alteration in specific factors controlling the characters of the plant or its composition with respect to certain ingredients.

Mass selection compared with individual selection.—The same process as illustrated in corn has been working in the increase in sugar content of sugar beets. In animal breeding the same problem is faced in advancing milk and butter-fat production in dairy cows and egg-laying ability in poultry. Ordinary mass selection, without regard to the heredity from the male side, is not very effective. With animals, the greater value of the individual as compared with that of the individual plant, has made it worthwhile to keep records of performance, making possible a more rigid selection. The Maine Experiment Station has demon-

strated that selection of high-laying hens, on the basis of trap nest records, has little result as compared with selection which takes into consideration the ability of the cock to produce high-laying daughters as well. Similarly, it is now generally recognized that the worth of the sire for a dairy herd depends on the milking records of his daughters.

Instability of mixed varieties.—Pure lines of self-fertilized plants are more stable than mixed varieties, which may contain a number of different pure lines. They are also more permanent than any cross-fertilized species. The changing, or "running-out," of varieties is illustrated by wheat. It is a common experience in the arid Southwest that the clear, hard, winter varieties, which give good results in the Wheat Belt, tend to become soft and opaque when grown for a number of years in warmer climates. This is generally considered as an environmental effect, but Freeman has suggested another possibility. Ordinary varieties of wheat are composed of a number of strains, some of which are softer than others. In the wheat-growing districts, the translucent, corneous strains are more hardy and make up the bulk of the varieties. In Arizona, the soft types are more productive and tend to increase until in a few years they practically supplant the others and the variety is apparently changed over into another sort. This change is merely a substitution of one kind for another. Soil and weather conditions do have some effect upon the texture of the wheat grain; but if Freeman's interpretation is correct, much of the supposed degeneration of varieties in southern regions can be prevented by propagating from pure lines.

Differential productiveness.—Such changes in plants, or instances of the running-out of varieties, as this phenomenon is sometimes called, are due to differential productiveness rather than to actual climatic effect. Dent varieties of corn, when grown in the North, tend to change over into a more flint-like type. Most of this is due to the fact that seeds in a typical dent ear are closely crowded

together and do not dry out rapidly. Hence, in the short growing seasons and cool falls of the northern region, the more flint-like ears mature better and consequently germinate more completely the following season. Therefore, in time, corn with round, corneous seeds and ears with rows widely spaced is the outcome.

With animals, production may be greatly curtailed by treatment, not only as a direct environmental effect, but as an agency in controlling the rate of propagation of different strains. High egg or milk production is dependent upon the most favorable conditions. Without this opportunity pure-bred stock may be less valuable than scrubs. The object of the breeder is to search out the most desirable strains in the environment which is best suited to bring their qualities to the highest expression.

Summary.—Selection, with animals as with plants, must deal with the individual, taking into consideration transmissible traits which it may have received from its ancestors but which it may not exhibit itself. Plant and animal populations are, therefore, complex. In self-fertilized plants there may exist a number of homogeneous types, as in a field with a mixture of wheat, rye, and oats. The function of selection is merely to sort out the most desirable of these component parts and propagate from them alone. Where cross-fertilization takes place the situation is much more difficult, because in addition to a mixture of different types, these elements themselves are in an unstable condition.

The genotype conception focuses attention on the individual organism and the single factor as the basis for selection. Mass selection can never be as effective as individual selection, because many forms having the same degree of development behave quite differently in transmission. It follows that visible characters are not reliable guides by which to ascertain the actual germinal composition of a plant or animal. This can only be accurately known by the progeny performance record.

CHAPTER X

HYBRIDIZATION IN PLANT AND ANIMAL IMPROVEMENT [1]

THE function of hybridization is to rearrange already existing characters, thereby bringing together qualities, scattered about in different forms, into one or a few individuals which represent the beginning of a new variety or a new breed. How the common fruits, flowers, and vegetables of our gardens, and domestic animals in the fields and about the house have been multiplied into endless kinds, by a recombination of a relatively few types, becomes apparent when the history of any particular group of plants or animals is reviewed.

History of the dahlia.—The dahlia is a garden flower popular because of its easy culture, simple vegetative propagation, and wealth of colors and forms. The fact that the plants can also be easily grown from seed, giving an astonishing array of markedly different flowers, has made this a fascinating subject for experimentation by the amateur gardener and has greatly increased the number of well-recognized varieties. The dahlia was first generally cultivated in Europe shortly before 1800, having been introduced from Mexico where it had been cultivated for a long time. According to Safford, several distinct wild species of dahlia exist in Mexico. He also states that both double- and single-flowered forms were cultivated there and introduced into Europe. In 1814 there were listed some 12 well-marked color types. Twelve years later, the number of varieties had increased to 60 through recombinations of the

[1] This chapter in an abridged form was published in *Scientific Monthly*, Jan., 1922, and is reprinted here by permission.

existing color varieties with the double-flowered condition, and new shades of color were also brought out by crossing and doubtless by mutation as well.

The most important event in the history of dahlia culture occurred in 1872, when a Hollander by the name of Van der Berg received a box of miscellaneous seeds, plants, and roots from a friend in Mexico whose name is now unknown. One of the roots was a dahlia which produced a blood-red flower of a shape entirely different from any seen before. This was the famous original cactus dahlia, so named because of its resemblance to the Showy Cactus. This single plant, hybridized with the many different varieties already at hand at that time, has to a large extent made possible the truly marvelous flowers of to-day.

Variation in dahlias.—There are now eight main types of dahlias, based on flower conformation. These are the **single, duplex, ball, cactus, decorative, peony-flowered, collarette,** and **anemone-flowered** dahlias. Classification is based on the number, size, form, and arrangement of petals. In some the petals are flat; in others they are curled, rolled, or quilled. The flower heads may be completely covered with petals, partly covered, or with but a single row of petals. A combination of large outer petals with a row of small petals, often of different color at the center, gives the collarette type. A single row of broad outer petals, with the central disk covered with small tubular petals, is the newest creation, known as the anemone-flowered or pincushion type. Besides these main classes there are numerous subdivisions based upon size of flower and growth of plant. These include dwarf forms and plants with long-stemmed and short-stemmed flowers. Colors are as profuse in dahlias as in almost any cultivated flower. They occur in self-colored patterns and in variegations which are classified into five different types, as shaded, edged, margined, striped, and mottled. How the individual variations first arose is, in most cases, wholly unknown; but, when they had once been found, it is not difficult to

see how by the recombination of all these different flower forms, colors, and patterns, together with differences in the growth of plants, the more than 3000 named varieties could be developed in 150 years.

The development of the sweet pea.—The sweet pea is another flower which has been marvelously developed in recent times. According to Beal, at the Cornell Station, this flower was first brought into general cultivation about 1700. As far as known, it developed from only one wild species and this was uniform in flower color and shape. After it had been in cultivation for some time, several well-marked changes were noted in flower color and color pattern. These different forms, crossed together, gave rise to still other types. Somewhat later the position of the petals changed from erect to recurved or hooded, presumably by mutation. All the previous color types could then be had in the hooded form as soon as the necessary recombinations were made. Later the Spencer type, with waved petals, originated and this variation has greatly extended the list of varieties. In habit of growth, there is the original tall-growing form from which there has been derived by abrupt changes the bush and dwarf or Cupid forms, and these in turn have somewhat different characters as seen in the prostrate Cupid and erect Cupid.

These main character differences of flower color, color pattern, flower form, and plant habit have, through reassortment brought about by crossing, given rise to named varieties running into the thousands. In the Spencer group alone, there are over 500 varieties showing differences in colors, shades, tints, patterns, and shapes. A relatively few factor changes have made possible this profusion of flowers.

Factors influencing the origin of varieties.—Horticultural achievements have not always been developed by intentional hybridization. Natural crossing, allowing for recombination between different varieties growing together, has undoubtedly been responsible for many of the new

forms. Even plants which are generally self-fertilized are occasionally cross-fertilized naturally, and this makes recombination possible; and the fact that such plants are rarely crossed and are therefore uniform makes conspicuous any off-type plants resulting from crossing. Domestication gives a plant or animal a far greater opportunity for further improvement as compared with wild forms, because of the immense numbers grown and the fact that these are under close observation. Careful culture also preserves many new forms which would be exterminated in the open. Those plants whose valuable part is comprised in conspicuous flowers or definitely marked seeds are more extensively multiplied into different varieties than those plants which are not so easily catalogued. Roses, tulips, and irises are a few notable examples of flowers which are widely diversified in form and color. Among the vegetables, beans are listed in almost endless variety, because the seeds, which are well marked in color and pattern, and the characteristic pods make the different varieties easily recognized, with the result that they are generally kept true to type.

An illustration of the result of natural crossing.—The way in which many varieties of garden and field crops originate is well illustrated by a natural cross of a commonly cultivated variety of garden beans. From a plot of Dwarf Horticultural beans, the seeds of which are characterized by splashes and stripes of irregular red bands on a light background, a few off-type seeds were found when the crop was shelled. These seeds were densely marked with a thick mottling of dark brown. There were only a few of the seeds among many hundreds of thousands of the Horticultural type, but they were very conspicuous on account of their darker color and altered pattern. They were produced by natural crossing, which had taken place the year before as the plants were grown adjoining plants of other varieties. This was proved to be the case when the odd-looking seeds were planted and the resulting seeds harvested. Almost every plant was different in color and

markings of the seeds. Representative seeds from a number of these plants are shown in Fig. 104.

Of the seeds shown in the illustration, those having the same markings differ strikingly in color. The differences are abrupt. Although there are eleven distinct kinds of seeds in this lot, it can be seen that they are made up of different combinations of color and pattern. In arrangement of color there are three types: self-colored, splashed,

FIG. 104.—The result of natural crossing. The eleven types differing in color and markings were grown from off-type seeds (above at the left) found in a field of Horticultural beans (above at the right).

and mottled. The colors are cream, tan, brown, and red. Only a few of the many possible combinations of these characters are expressed in this small number of plants. Each seed is a possible beginning of a new variety. Some of the combinations are undoubtedly heterozygous and will break up in later generations. One of the seeds is an exact reduplication of the parental hybrid seeds. Another goes back to the one known grandparent. What the other grandparental variety was can only be conjectured.

In addition to those striking differences of color and markings, the seeds differ somewhat in size and shape. Whether these are genotypical differences or merely modifications due to the growth of the plant can only be told by further testing. The plants which produced these seeds differed in no less degree. They were yellow or green podded and the pods were flat or round. They were diverse in time of blooming and ripening. They were also unequal in productiveness, hardiness, disease resistance, stringiness, and toughness of the pods. These are the more important qualities, but they are not so surely recognized as the noticeable seed characters.

Natural crossing an important agent in diversification.—Natural crossing occurring in this manner has been the most important agency in the multiplication of varieties. Striking variations, such as those noted in the beans just described, attract the fancy of the gardener, and the odd seeds are saved and sown. The unusual features may or may not persist. Some of them may be an improvement over existing sorts. The seed from the most promising plants is again saved, and since beans are largely self-fertilized the hybrid combinations of characters are quickly reduced in numbers. In the course of several years, uniform and constant strains are established; that is, they soon come true to type. The best of these strains are selected and a new variety has been created or rather re-formed. Further testing shows whether the new variety has sufficient merit to be worthy of general cultivation, and if it has it soon finds its way into the seed catalogues. Such in brief is an outline of the history of nearly all the commonly cultivated vegetables and flowers.

It is generally thought that selection has brought out these new forms. Such is indeed the case, but the variability induced by crossing has made the opportunity for effective selection. Those characters which really determine the value of a variety, such as hardiness, productiveness, and quality, and which are dependent upon all parts

of the plant, are so complex in mode of inheritance that it is not at once apparent that recombination of definite hereditary factors takes place in these characters just as surely as in color and pattern. The changes are usually small in degree, and the characters are more easily influenced by the external conditions. For that reason selection is the means of sorting out the best hereditary material, and with many plants and all animals selection must always be continued to maintain improved varieties at a high level.

Universality of variation by combination.—In one sense, hybridization produces nothing new. It merely takes materials which are already in existence and by putting them into different associations makes forms which have never been seen before. This is a universal method of diversification. The Roman alphabet has less than 30 symbols; yet the English language alone has over 450,000 words. All chemical compounds are different groupings of about 80 elements. That hybridization can produce nothing new is equivalent to saying that architects can create no new buildings because they have to use the same bricks and boards, cement and sand they have always used or the musician can write no new songs because he has at his disposal only the same set of notes and modulations. The possibilities for creation by combination are practically unlimited. Especially is this true in organic substances, where each new compound forms a new unit which can associate with other units to form new compounds. The hereditary factors, as far as known, are compounds so complex that their formulas can not as yet be written.

History of some recent breeds of poultry.—The higher animals are always cross-fertilized. The history of the more recently created breeds of animals shows that hybridization has furnished the beginnings; controlled matings and careful selection have followed this up. Poultry furnishes many excellent examples of the part played by hybridization in animal breeding. The history of the development of the general-purpose breeds of American

origin is better known than that of other breeds, although all are not agreed as to the foundation stocks of these American breeds. For the Barred Plymouth Rocks, one of the most popular all-round breeds among the farmers of this country, the Dominique furnished the pattern and the Black Java or Black Cochin the size. It is believed that the Minorca and Brahma were also used. The first specimens were exhibited in 1869. The type of body has been fairly well fixed, and Plymouth Rocks are now obtainable in several different colors and patterns.

The Rhode Island Red remained for a long time a farm fowl, and was not considered a distinct breed or taken up by the " Standard " breeders until after it had established its reputation as a utility fowl. It is one of the most variable breeds in color, because of its extremely mixed origin. Although the material used is somewhat in doubt, both Asiatic and Mediterranean stocks were crossed on native breeds. According to one writer, Red Malay, Shanghai, Chittagong, Brahma, and Leghorn were crossed in every conceivable way. As the red color distinguishes the Rhode Island Red from all other common fowls, it was easy to establish a new breed. It illustrates well the point that breeds are based on a few outstanding, easily-seen characters and the more valuable features are built up around them. Such has been the origin of the more recent breeds. With various modifications, it is probably typical of the beginning of many breeds of poultry whose past history is now unknown.

Origin of popular breeds of sheep.—Sheep are among the oldest of domesticated animals, and nowhere have they been more highly developed than in England. Most of the modern mutton breeds with which we are now familiar had their origin there. Some, such as the Southdowns and Dorsets, were so excellently formed since very early times that their beginnings are not known. The former has very fine qualities, as indicated by its widespread popularity and by the fact that it has been used in crossing with other

local strains to produce many of the now prominent breeds. For example, it is generally believed that the Shropshires are the result of crossing Southdowns with the native horned, black-faced sheep of Shropshire. The Leicester and Cotswold breeds also are thought to have contributed something to the prominence of this famous race. Similarly, the Oxford sheep grew out of the intermixing of Cotswolds and Hampshires, while the Hampshires in turn got their start in crosses of the native Wiltshire and Berkshire sheep, followed by judicious use of Southdown rams. Later, the Sussex sheep, which had a somewhat similar origin, were united to make the material out of which have come the modern Hampshires. To-day, in the western states, the Department of Agriculture is endeavoring to unite as many of the good qualities of the Lincoln and Rambouillet breeds as possible, to form a new one for which the name of Columbia is proposed.

Should one examine the history of the creation of the present-day breeds of swine, he would find that much the same line of development has taken place. Crossing to bring together desired characters from different types brought out in different places and to serve different purposes, followed by intermating and back-crossing of the progeny and close selection towards a more or less fixed objective—such has been the almost unvarying recent history of the smaller and faster-breeding animals. The larger and more slowly reproducing farm animals, the cow and the horse, are not so easily handled in this way. The creation of new varieties, which means the culling out of enormous numbers of inferior individuals, is too expensive a procedure to be undertaken without good reason. But is it not a logical assumption, from the known history of the smaller animals, that crossing has played an equally important part in the early development of the horse and the cow, which had already reached a high plane before the written history of the breeds began? Few breeds have resulted directly from hybridization. The general pro-

cedure has been a gradual infusion of heredity from different races, and from this there evolved gradually a type which later became recognized as a new breed.

The Percheron horse.—It has long been stated that the chief contribution of France to agriculture, the Percheron horse, reached its highest development following the intro-

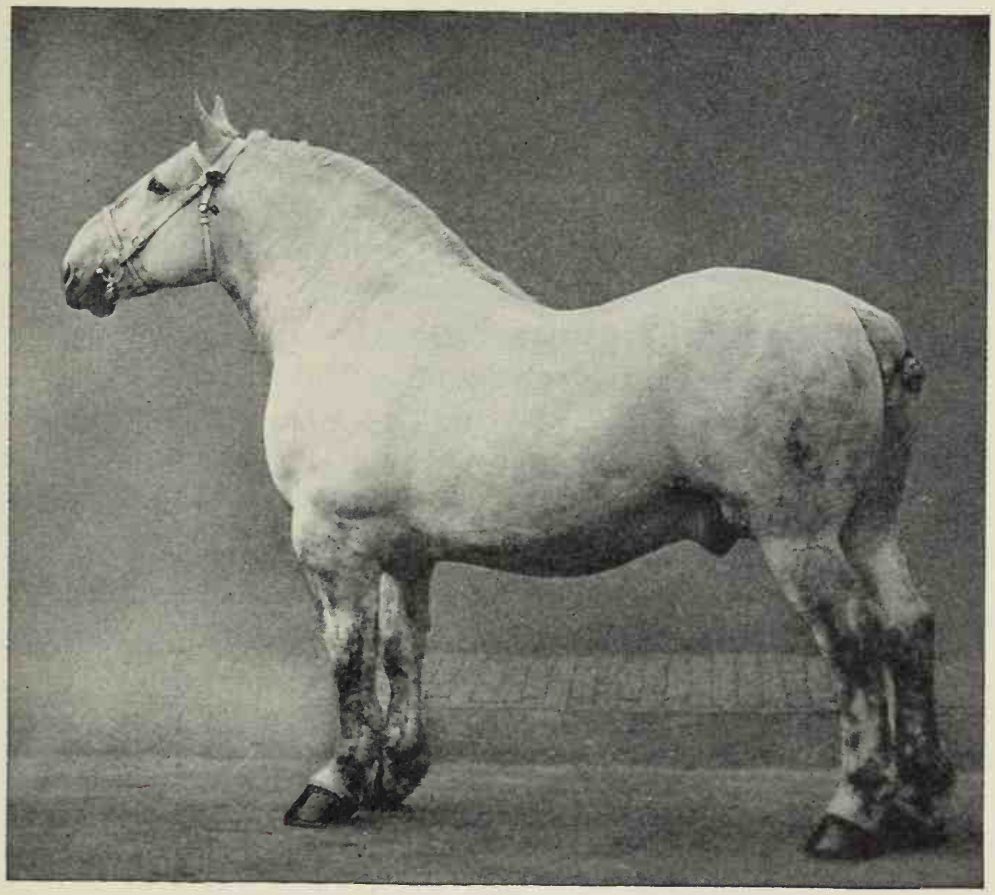


FIG. 105.—"Rectorat," a leading representative of the Percheron breed of horses. (Courtesy of the Percheron Society of America.)

duction of the Arabian horse among the native heavy horses, after the defeat of the Saracens in 732. Sanders and Dinsmore, recent writers on the Percherons, are, however, strongly of the opinion that the influence of the Arabian horse has been greatly exaggerated, and even question whether or not mixing ever occurred in any important amount and persisted. They base their chief argument

on the fact that the color pattern of the Percheron is distinct from the markings of the Arabian. Unless this objection is supported by more convincing evidence, it can hardly be conclusive, as it is not to be expected that a complex parental pattern would be recovered completely from such a mixture unless it was made a specific object in selection. It is a fact that the Arabian war horses were present in France in large numbers. It can hardly be doubted that they were frequently crossed with native stock. How many of their desirable qualities have persisted is largely to be conjectured. But the Percheron differs from the other heavy draft breeds most noticeably in neatness of body and lightness of foot, qualities which could very easily have come from Arabian ancestry.

Development of varieties of wheat.—The history of the development of leading varieties of cultivated plants closely follows that of animals. Naturally a great deal of attention has been given to the upbuilding of wheat, because it is the most important bread-making cereal in Europe and America. Most of the varieties now widely grown have come from individual plant selections from older varieties. A beardless head in a field of bearded wheat, or a blue-stemmed plant in colorless sorts, attracts attention. Seed may be saved from such plants, and if the progeny prove to be sufficiently distinct and better a new variety is in process of formation.

The Scotch Fife wheat has been popular in the Northern States and Canada. Its origin is typical of many other varieties. David Fife, living in Ontario, received a quantity of wheat which had come originally from Russia. He planted it in the spring, but it proved to be a winter variety and consequently only three heads ripened, these belonging to a single plant. Sown again the following spring, the wheat proved remarkably resistant to rust, and from these few plants the seed was rapidly increased and widely grown. From the crossing of Fife with an introduction from India, known as Calcutta Red, followed by selection

and careful testing, has come Marquis. Produced by William Saunders of the Canadian Experiment Station at Ottawa, Marquis wheat is now grown on fully 15 million acres and is the most important plant-breeding achievement, in point of money value, that has yet been made.

Fultz is one of the best known of the older varieties of American wheat. It originated from three heads of beardless wheat in a field of the Lancaster variety. Later, S. M. Schindel, of Hagerstown, Maryland, crossed Fultz and Lancaster, and out of this came Fulcaster, which is a bearded, semihard, red-grained wheat, quite resistant to rust and drought. It has been grown generally over the country but particularly in the region from Pennsylvania to Oklahoma. The possibility of recombining disease-resistance with valuable qualities from other varieties has been well established by Biffen in England. Among a large number of different wheats tested at the Cambridge experimental farm, one was found which was apparently quite immune to rust (*Puccinia glumarum*). Even when grown among badly diseased plants, it was free from infection. Another variety showed no plants without the disease. All the plants of the first cross of these two varieties were rusted badly; but in the second generation plants free from disease were found, and from these, strains were established which had a high degree of rust resistance and at the same time were more desirable than the original immune variety used at the start.

A. E. Blount, of the Colorado Experiment Station, made a large number of wheat crosses and developed some popular varieties which are grown both in this country and in Australia. There they have been used as the parents of some of the most valuable varieties grown. William Farrer, in New South Wales, has had remarkable success in producing valuable varieties of wheat by crossing. Federation is the most prolific and widely grown wheat, and two other varieties, Bobs and Comback, likewise the result of crossing, have unsurpassed milling qualities.

Early Genesee Giant, which has been popular in New York and Pennsylvania, was the result of most extensive crossing performed by A. N. Jones in New York State. Sixteen different varieties or unnamed hybrids entered into its pedigree, as shown in Fig. 106. Crossing was carried on extensively, with the definite object of producing a wheat having a high proportion of gluten, in order to make a bet-

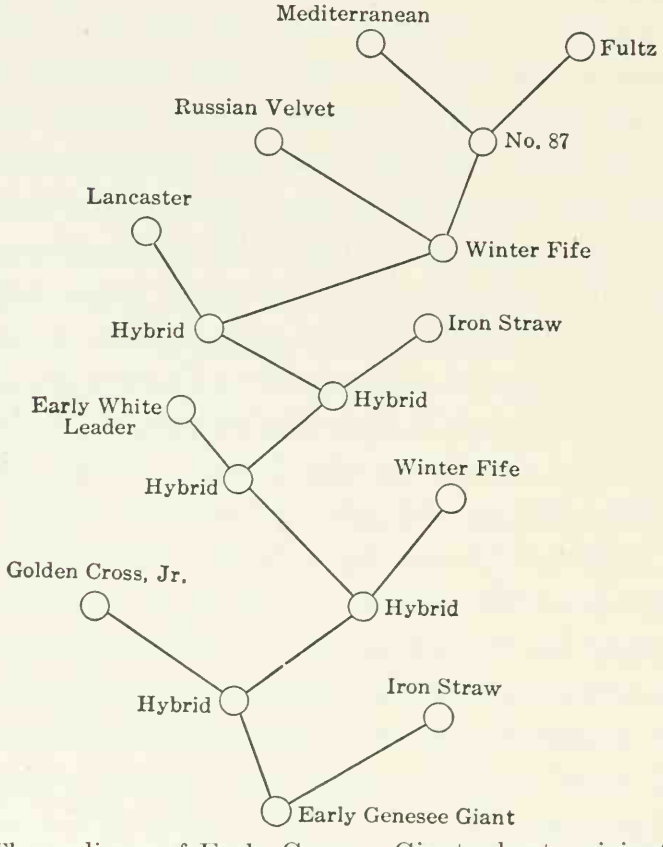


FIG. 106.—The pedigree of Early Genesee Giant wheat, originated by A. N. Jones in New York. (After Carleton in U. S. Dept. Agr. Bull. 24.)

ter bread wheat than the soft, starchy varieties generally grown.

Natural crossing among potato varieties.—One of the best illustrations of a successful plant-breeding enterprise, from the standpoint of practical results obtained, was the potato varieties produced by E. S. Carman, late editor of the *Rural New Yorker*. Rural Blush, Rural New York No. 2, Carman No. 1, Carman No. 3, and Sir Walter Raleigh

are varieties which came from a collection of 62 varieties which were gotten together for the purpose of crossing. Artificial pollination proved to be impossible on account of failure to find good pollen, but from seed bolls naturally formed (undoubtedly many of the seeds resulted from crossing between varieties) a large number of seedlings were raised and from these the five best were distributed after careful testing. It is stated that at one time 80 percent of the potatoes grown in this country were either Carman's productions or seedlings from them. He accomplished what he set out to do in producing a better potato than the old Early Rose and Peach Blow.

The early development of popular corn varieties.—That natural crossing has played a large part in the production of corn varieties of all kinds is apparent. The ease with which pollen is carried by the wind, and the practice of growing many different sorts near together, or even in the same field, maintain a constant state of out-crossing and a resultant variability out of which selection can start new departures.

The history of Reid's Yellow Dent, now one of the most popular varieties throughout the Corn Belt, is typical. Robert Reid, from Ohio, brought with him to Tazewell County, Illinois, seed of a local variety known as Gordon Hopkin's corn. This was planted in Illinois in the spring of 1846, and did not thoroughly mature; consequently, the seed did not germinate well the following year. The missing hills were replanted with an early variety known as Little Yellow corn. The corn has not been purposely mixed since then, but by selection the type of this well-known corn has been developed.

Origin of dent corn.—The dent type of corn was not produced for the first time by Reid as this kind of corn has been known since very early times, having been reported by Sturtevant to be in the possession of the Powhattan Indians in Virginia as early as 1608. The characteristic indentation of this most productive kind of corn is due to a corneous outer layer surrounding a center of soft starch.

On drying, this soft starch shrinks more than the hard starch outside and thus brings about the depressed and folded tip from which the type gets its name. Flint corn has more hard starch, the soft starch being limited to a small area about the embryo. Types of corn are known which have no hard starch and others which have no soft starch. Crossing these two types gives kernels of both dent type and flint type. Early historical writings indicate that modern dent

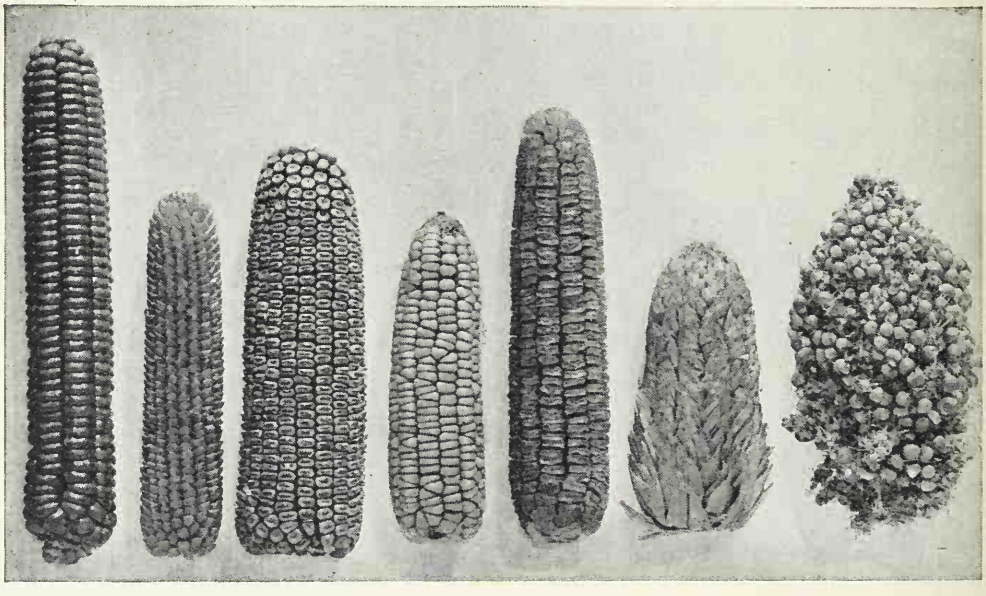


FIG. 107.—The principal agricultural sub-species of maize. They are, from left to right, flint, pop, dent, flour, sweet, pod and branch corn.

varieties originated from the mixing of floury and flinty types.

Rapid multiplication of varieties of sweet corn.—A familiar example of the rapidity with which varieties can be produced by crossing is furnished by the yellow varieties of sweet corn which have been introduced during the past few years. Practically all of them originated from a small-eared, yellow-seeded variety known as Golden Bantam. This variety for some time was little known and not appreciated, because its yellow color differentiated it from all other varieties of sweet corn commonly grown and made it appear like field corn. It was finally realized that Golden Bantam

was somewhat more tender in texture and better flavored than other varieties. Its small ears and low yield induced many to cross it with the larger-growing kinds and then to regain the yellow color combined with larger stalks and ears and with as much of the quality of Bantam as possible. The yellow color is easily regained, because in the second generation following the cross of yellow and white one seed in every four will be pure yellow, but it is more difficult to retain the sweetness and tenderness of Golden Bantam in a larger and more productive corn. Some success has been achieved, judging from the popularity of the new yellow sorts, such as Goldenrod, Golden Giant, Buttercup, Bantam Evergreen, and a host of others which represent a recombination of the characters of Golden Bantam and such standard varieties as Evergreen, Howling Mob, and Country Gentleman. Yellow color has now become the badge of honor among sweet corns.

The climbing American Beauty rose.—The number of new roses continually being offered is so great that only an exceptional variety or novelty creates much interest. Within recent years the climbing American Beauty has attracted considerable attention. This variety was developed by James A. Farrell, West Chester, Penna., from a cross of American Beauty with an unnamed seedling of *R. Wichuraiana* and Marion Dingee. It possesses the large flowers and long stems of one parent combined with the profuse bloom and rampant growth of the other.

The strawberry as an example of systematic hybridization.—The strawberry is the best example of systematic hybridization which has given valuable practical results. It is stated that of the 200,000 acres of this fruit grown in the United States 90 percent are planted with varieties that resulted from carefully planned experiments and not from chance seedlings. Senator Dunlap, which has long been a widely grown northern variety, was brought out by J. R. Reasoner of Urbana, Illinois. It was the result of crossing and selecting, systematically carried out. Klondike, which

covers eight-tenths of the strawberry acreage in the South, was originated by Robert Cloud of Louisiana, who has also propagated other good varieties. Hubach and Bauer of Judsonia, Arkansas, have independently developed many noteworthy strawberries by crossing.

Physiological limits.—Practically, there are limits to what can be done by hybridization and selection, although no one can say exactly what these limits are. Certain characters are antagonistic. Fruit growers dream of an apple with the productiveness and hardiness of a Ben Davis combined with the delicacy, sweetness, and flavor of a McIntosh or Northern Spy. Yet the tough skin, thick cell walls, and low sugar content of the Ben Davis are probably the very things which make it resistant to disease and able to produce abundantly under adverse climatic conditions.

The plant breeder who sets out to produce a wheat with the best milling and baking qualities, together with maximum yielding capacity, and resistance to disease and severe climatic conditions, has a task which is extremely difficult if not impossible. Likewise the animal breeder can not expect a rapid maturity and tenderness of flesh together with ability to withstand adverse conditions.

Those qualities which have been developed in domesticated forms are the ones that make them less able to cope with their surroundings. Wild species, on the other hand, are constantly selected according to their ability to endure climatic extremes, pests, and diseases. Their only concern is to live and provide for reproduction. Anything beyond this is a handicap. Moreover, there are limits beyond which it is impossible to go. Obviously, a cow can not be expected to give milk which is all cream, neither can a sugar beet be all sugar. What the limit is, can not be closely approximated. Certainly, if one were familiar with only the wild gourds, he would be inclined to think a pumpkin or watermelon weighing over 100 pounds a fantastic dream not to be realized. The lime tree gives no indication that a near relative can produce a fruit as large

as the tropical grape fruit, which often weighs over 10 pounds. Between the wild cattle in the parks of England and the prize-winning Shorthorns and Herefords at the live-stock expositions there are almost incredible differences.

Variability due to hybridization of different species.—Selection, even in the long period of time in which plants and animals have been domesticated, could not bring about these vast differences, were it not for the variability made possible by frequent crossings between widely diverse stocks. When the origin of the familiar cultivated plants and domesticated animals is investigated, it is significant that nearly all of the more important ones have been derived from more than one wild species, and these usually from separate regions.

Origin of the domestic fowl.—As an example of a valuable animal which has been cared for in nearly every part of the world, the domestic fowl can be taken. It has long been thought that all the diverse breeds and types of chickens came originally from the Jungle Fowl of India, southern China, and the East Indies; but it is now believed that the unknown ancestor of the Aseel, or Malay Fowl, which has been bred in captivity for over three thousand years, is also in part responsible for the present divergent development exhibited by the many different breeds and races.

According to Davenport:

"The Aseel has many points of difference from the Jungle Fowl and brings in a whole set of characters that our domestic races have and the Jungle Fowl lacks. Thus the Jungle Fowl is a slender, agile bird with long wings, erect tail and a good flyer; while the Aseel is a very broad, heavy bird with short wings, drooping tail and unable to fly. The Jungle Fowl has a long slender beak, that of the Aseel is short and thick. The comb of the former is single and high, that of the latter triple (or 'pea') and low. The former has slender olive-colored shanks; the latter thick and yellow shanks. The Jungle Fowl has a red eye; that of the Aseel is pearl colored. The Jungle Fowl has the well-known English Black-breasted Red Game pattern; the Aseel is

mottled. The Jungle Fowl is the foundation stock of our nervous, flighty, egg-laying races—the Leghorn, Minorca, Spanish, Andalusian, etc.—the races that first spread over Europe, probably from the stock that was brought back from Persia by the expeditions of Alexander the Great. All of these races ordinarily carry the determiners of the Jungle type of coloration. Representatives of the Aseel type (which had long been established in Eastern India and China) were brought to America, becoming the ancestors of the Asiatic breeds and the fine general-purpose breeds—the Plymouth Rocks, Wyandottes, Orpingtons, etc. Such do not regularly carry the Jungle type of color pattern. In one case on the contrary—namely, in the Buff Cochins—they introduced a new kind of color which (arisen in China fifteen hundred years ago) has never been produced independently since. The fowl of the Aseel type are poor egg layers, but their stocky build and great size make them unrivalled as table birds."

Many wild species of birds which resemble the domesticated fowl are found in the East Indies. Recently Lotsy and Kuiper have presented results obtained by Houwink, which show that at least three of these wild species can be inter-crossed and give partially fertile offspring. Some of the crosses were made with great difficulty and the offspring were fertile only when crossed back with one or the other wild species. Among the three species tested is *Gallus bankiva*, which crossed easily with domesticated fowls. Some of the characteristics of the domesticated hen are observed in these wild species.

Variation among dogs.—Of all domesticated animals, the dog is probably the most varied in size, in form, in color, and in covering. Ranging from the Poodle and Dachshund to the Bulldog, Greyhound, and Great Dane, the dog has been the companion of man in nearly every part of the world. The near relatives of the dogs are numerous, and although they are truly wild many are capable of being tamed and most of them will cross with some breeds of dogs. The timber wolf of Russia, the jackal of Europe, Asia, and Africa, the coyote of North America, and the dingo of Australia have all probably contributed something to present-day forms. Even the fox is quite like the dog

in certain respects and may be remotely connected with some of our dogs.

Development of the pig.—The pig is a widely domesticated animal which reached its greatest development when the breeds of Europe and Asia were brought together and their qualities intermingled. Early in the seventeenth and eighteenth centuries, Chinese hogs were introduced into Europe, and from these sources there grew the great

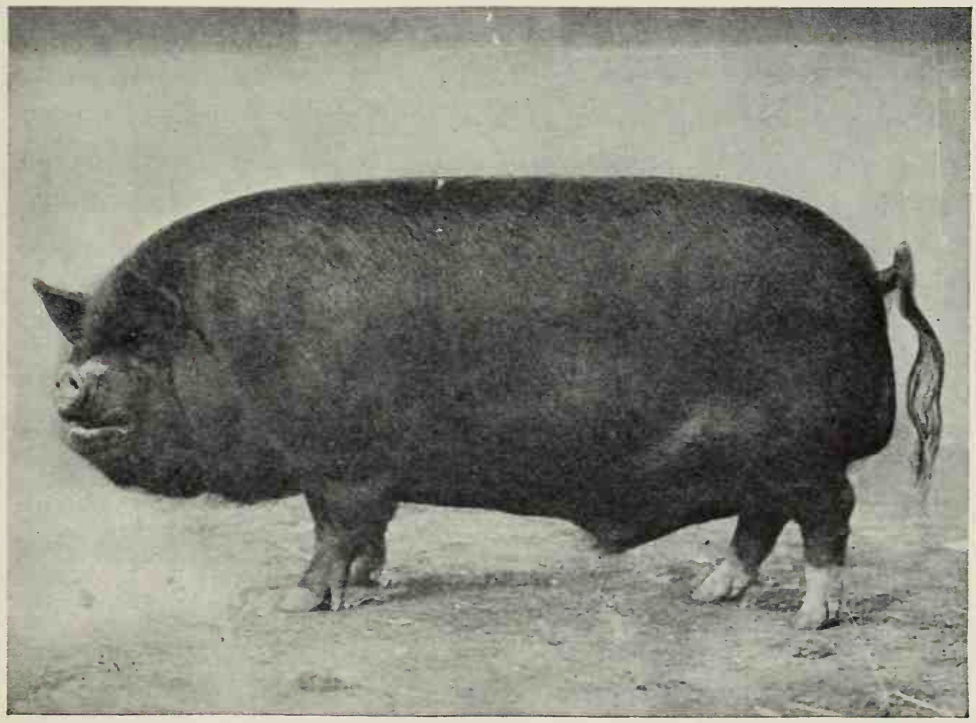


FIG. 108.—"Longfellow's Double," a leading representative of the Berkshire breed. (Courtesy of Hood Farm.)

breeds of Yorkshire, Tamworth, and Berkshire. Other breeds, such as Poland-China and Duroc-Jersey, have been perfected and named in this country, but their foundation stock came originally from England, the Continent, and Asia. The wild ancestors of the pig are considered to be the wild boar of Europe and Africa (*Sus scrofa*) and the Indian wild boar (*Sus cristata*).

One could extend this recital of the origin of tame animals to show that in the case of sheep there are at least six wild

species which could have been drawn upon, and a host of more distantly related forms; and that with cattle domesticated forms are classified in two species, European and East Indian, and there are any number of closely allied wild species. The horse has only one wild relative, a small animal, resembling a Shetland pony, which has been found on the plains of Central Asia. Either the horse has had a comparatively simple origin, or else it has been cared for so long that its other prototypes have been lost. The pigeon also has a large number of varieties whose origin are commonly attributed to but a single wild species. The same can be said of the honey bee. The domesticated turkey has been recently taken from the wild, and there is no evidence that species hybridization has played any important part in its development and diversification under domestication.

The flexibility of domestic animals.—Although much of the history of domesticated races is largely surmised, there can be no doubt that the intercrossing of different species from separated regions has played a very important part in their great alterations to suit the needs of man. Desirable qualities existed in several forms of allied animals in different regions. Tribal migrations and commercial intercourse furnished the means for bringing them together and, as far as they were sexually compatible, crossing undoubtedly was utilized to combine good features. Moreoever, the crossing and resulting variability brought out new possibilities not before realized. How else can one account for the great flexibility of domesticated races as contrasted with wild species?

Species-hybridization among plants.—The same occurrence of species-hybridization is largely at the bottom of the development of cultivated plants. Some forty-two distinct species and sub-species of cotton, coming from both the Eastern and Western Hemispheres, have been described. Many of these are cultivated in various parts of the world. In this country, 99 percent of the cotton grown is the short-

staple upland type and the remainder is the long-fibered Egyptian or Sea Island cotton, so called because it was formerly grown successfully only on the islands off the South Atlantic coast, and parts of the mainland. It is now grown in Egypt and in the irrigated valleys of the Southwest.

Origin of the cultivated cottons.—Authorities differ as to the origin of the cultivated cottons. Cross-pollination of the plant is easily effected by insects, and hybridization between species introduced into new regions has certainly taken place. Watt considers upland cotton to consist of various hybrids between *Gossypium herbaceum*, *G. mexicanum*, and *G. hirsutum*. The first is the Old World form, which probably originated in northern Arabia and Asia Minor. The other two species are natives of the southern United States, the West Indies, and Mexico. Sea Island cotton is generally considered as *G. barbadense*, originating in Barbados or other West India islands, but Watt is convinced that it too has had a mixed beginning. He considers it as having been developed somewhere in South America and having the Peruvian or Andes cotton, *G. peruvianum*, as one parental stock.

The indications of a mixed origin for corn.—Indian corn is perhaps the best example of a widely cultivated plant having apparently a single origin. Belonging to a small subdivision of the grass family, it has as its nearest wild relative teosinte, with which it hybridizes readily. Teosinte (*Euchlaena mexicana*) is a large semitropical grass which is sparingly cultivated and differs in many ways from maize. The seeds are borne in one-rowed spikes. If corn has been derived solely from teosinte there has been a remarkable sequence of changes, in that the original condition of two or more spikelets grouped together, which is typical of most cereals, has been replaced by the one-rowed spike in the pistillate inflorescences of teosinte and then regained in the paired-row condition in the ears of maize. Collins has pointed out that there exists in certain plants of pod corn

(*Zea mays* var. *tunicata*) a form with perfect-flowered terminal inflorescences, which strongly suggests another species as one of the original stocks. These perfect-flowered plants can not be distinguished by present botanical standards from a distinct tribe of grasses, the sorghums. In

FIG. 109.—The only wild relative with which maize will hybridize is teosinte (left), a large and luxuriant grass in its native home, Central America. The product of their union is shown in the center.

those characters in which maize differs most from teosinte it approaches the characters of this perfect-flowered pod corn. Certain other considerations also make it highly probable, although they do not prove, that maize likewise must be assigned a hybrid origin. The great variability and extreme plasticity by means of which corn is grown in many regions

from the edge of the arctics to the tropics, throughout the world, would be difficult to comprehend on any other assumption.

The intergradations of the rosaceous fruits.—Of all cultivated plants, the rosaceous fruits give the most unmis-

FIG. 110.—Maize differs from teosinte in many important features. In this perfect-flowered type of pod corn it approaches very close to a distinct tribe of grasses, the sorghums.

takable evidence of having been developed by means of species hybridization. Some thirteen wild species of apples exist in the temperate regions of the Northern Hemisphere. Many of these have characters which entered into the make-up of this widely cultivated fruit. The cherry-plum-

apricot-peach-almond group intergrades from one to the other so that it is impossible for the taxonomist to fix any exact limits to any division. Bailey lists 75 species and over 150 horticultural types of plums alone. From six native species, 300 named varieties have been produced since the settlement of the New World.

Complexity of the rose.—The rose itself is both the despair of the systematic botanist and the delight of the gardener bent on originating new forms. The rose grows wild in nearly all parts of Europe, Asia, northern Africa, and North America. The taxonomists have great difficulty in defining a rose species. Bentham and Hooker list 30, while Gandoger describes 4266 species from Europe and western Asia alone. Most botanists recognize over 100 species. The more common horticultural types and the specific names under which they go are as follows:

Horticultural Types and Species of Rose

Ayrshire	*R. arvensis*	Dog	*R. canina*
Banks	*R. Banksiae*	Eglantine	*R. rubiginosa*
Bengal	*R. chinensis*	Memorial	*R. Wichuraiana*
Bourbon	*R. Borbonica*	Moss	*R. gallica* var. *muscosa*
Cabbage	*R. centifolia*	Musk	*R. moschata*
Champney	*R. Noisettiana*	Noisette	*R. Noisettiana*
Cherokee	*R. laevigata*	Prairie	*R. setigera*
Chinese	*R. chinensis*	Provence	*R. gallica*
Cinnamon	*R. cinamonea*	Scotch	*R. spinossima*
Damask	*R. Damascena*	Sweetbrier	*R. rubiginosa*

The names of the two principal groups of the large-flowered roses, such as the Hybrid Perpetuals and Hybrid Teas, denote their mixed origin. The latter group, of which the variety La France is a popular representative, is the result of back-crossing a hybrid combination of the Provence, Chinese, and Cabbage roses on to the tea-scented China rose. Wilson gives the deriviation of these, the most important cultivated roses as shown in Fig. 111.

Grape culture in America.—The development of the native varieties of grapes, after it was found that the European varieties were unable to thrive in the eastern

part of this country, furnishes one of the most interesting chapters in horticultural history. Many species of grapes grow wild in North America; they are easily cross-pollinated under natural conditions, and individual seedlings of some of these wild forms came very early into cultivation and are still grown. The principal native species and the most important varieties derived chiefly from them are:

Vitis labrusca	Catawba,	Concord
Vitis rotundifolia	Scuppernong	
Vitis aestivalis	Norton	
Vitis riparia	Clinton	

From these varieties as basic stock have come nearly all of the many excellent grapes now grown. Concord is

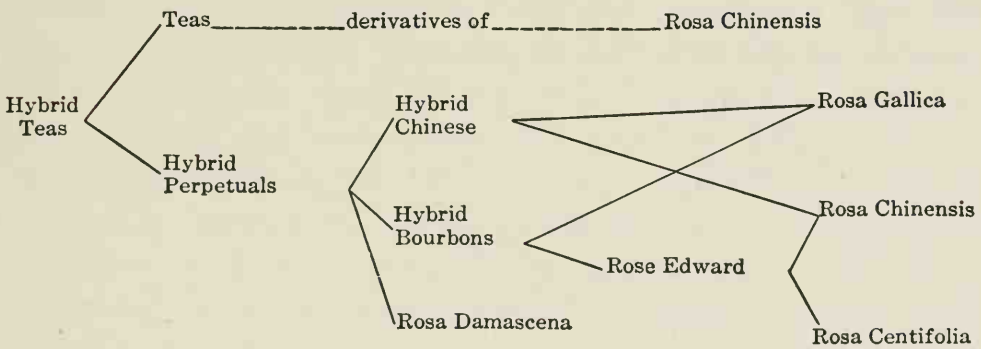


FIG. 111.—Derivation of the hybrid tea roses. (After Wilson in the Garden Magazine.)

the leading variety. In New York, 75 percent of all the grapes grown are Concords. This variety and its derivatives produce three-fourths of the grapes grown in the eastern region. The history of the Concord is obscure, but the evidence indicates that it is the product of a large-fruited plant of the wild fox grape (*V. lubrusca*) pollinated by a plant of the Catawba variety which was growing near by. The botanical characters of the Concord are almost wholly *labrusca* but some of the self-fertilized seedlings of Concord show strong indications of influence by *Vitis vinifera*, the European grape. Catawba, one of the assumed parents of Concord, is also a seedling of *labrusca*

brought in from the wild, but it shows even more indications of *vinifera* characters than Concord, in the vinous flavor of the fruit, susceptibility to mildew, appearance of occasional seeds, and especially in the seedlings of the Catawba, many of which resemble *vinifera* more than the parent. The Catawba was one of the first native grapes to be cultivated. It originated in 1819 in Montgomery County, Maryland, and is still widely grown. While it is not positively known, there seems to be little doubt that crossing took place between European varieties and the wild plants growing nearby. Large numbers of the *vinifera* grapes were grown at that time in an attempt to find some that would withstand the ravages of unaccustomed insects and diseases in the New World. These chance crosses gave size and sweetness, together with resistance, and made possible for the first time satisfactory grape culture. Hedrick in the "Grapes of New York" gives the derivation of all the leading varieties. In many cases the parentage is doubtful as many varieties have originated as chance seedlings. Out of 205 varieties, 74 are known to be the result of a combination of *V. labrusca* and *V. vinifera*. Eighty-eight varieties are more complex hybrids, but most of them have either *vinifera* or *labrusca* heredity in addition to other native species. The remaining 43 varieties listed as coming from single species are mainly seedlings of Concord, and this, as has been stated, is strongly suspected as being of a hybrid American–European origin.

The systematic production of new grape varieties is illustrated by the work of Roger, one of the early hybridizers. The American variety Carter was pollinated by Black Hamburg and Chasselas, two European varieties. A large number of seedlings were raised and from this lot 45 were chosen as sufficiently promising to be sent out for trial. From these a number of named varieties were placed on the market and some are still grown, Agawam being the most popular. The Concord, although the most widely cultivated grape at the present time, is somewhat lacking in

quality. It is exceeded in this respect by many varieties, such as Diamond, Dutchess, and Brighton, which have been derived from Concord by bringing in more of the qualities of the sweet European grape. The pedigree of one of these varieties, as shown in Fig. 112, is typical of the way in which modern grape varieties have been produced by hybridization.

Species of bramble berries.—Promising material, which has only begun to be utilized in the formation of better fruits, is at hand in the brambles, particularly the raspberries. They exist in three different forms, which are associated with color of fruit: the red, the purple, and the black. The purple sorts are unmistakably hybrids between

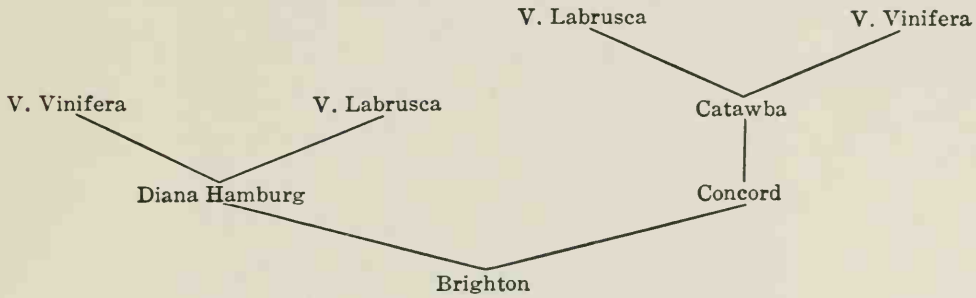


FIG. 112.—Pedigree of the Brighton grape.

the red and black varieties, as shown by recent crossing experiments at the Geneva Station. It has been generally considered that the American varieties of red raspberries were developed from the native *Rubus strigosus* and not from the European species, *R. idaeus*, but Darrow gives evidence that Cuthbert, the leading red sort, is a hybrid between these two species as it possesses definite characters of both. This variety originated in 1865, at Riverdale-on-the-Hudson; it was found growing near the edge of a patch of Antwerp, a European variety, and probably resulted from natural cross-pollination of this variety with the native wild species, giving it hardiness, vigor, and greater size of fruit.

The purple raspberries, represented by the most popular variety, Columbian, are a distinct horticultural advance as

they make possible the cultivation of a raspberry with something of the quality of the red sorts in the western plains, where the satisfactory culture of the true red is impossible. Columbian is attributed to the Cuthbert (red) and Gregg (black) raspberries, and is thus a combination of three species, as shown in Fig. 113.

Alfalfa.—Another specific instance in which hybridization has produced valuable plants is furnished by alfalfa. The profitable cultivation of this valuable forage plant in northern regions has been made possible by the development of winter-hardy sorts, such as Grimm, Canadian Variegated, and other varieties in this country, and Sand Lucerne in Europe. These are unquestionably the result of crossing the long-cultivated alfalfa of southern Asia and

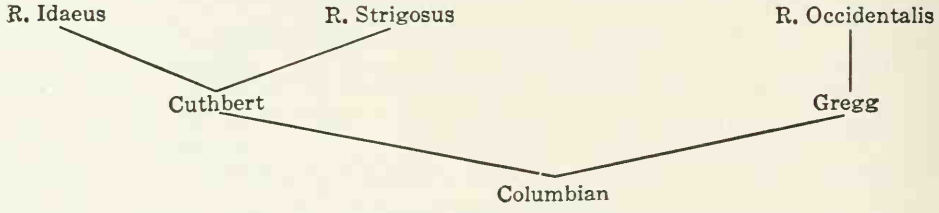


FIG. 113.—Parentage of the Columbian raspberry.

Europe with the hardy Russian *Medicago falcata*. This is shown by the variegated flowers, less curled seed pods, and more prostrate growth. Natural cross-pollination could easily have taken place as both types have been grown near together in Europe. Since they were introduced into this country by early settlers in Minnesota and other northern states, the selective action of the rigorous climate has developed extremely valuable alfalfas for these districts.

Recent crossing among animal species.—The opportunities for hybridization of species are not so evident with animals as with plants at the present time. Most of the types and breeds are well established, and experimentation with animals is so costly that it is doubtful if radically new forms will ever supplant them. Plants can be raised by the millions for the purpose of producing only a few of merit, without prohibitive expense, but with animals the

situation is different. One instance serves to indicate what the procedure has probably been in the past in the creation of new kinds of animals. The American buffalo crossed by domestic cattle has given a type with the hybrid name cattalo, which is promising as a range animal for the

FIG. 114.—Tree obtained in the second generation from a cross of the American chinquapin (*Castanea pumila*) and the Japanese chestnut (*Castanea crenata*), showing resistance to blight and early bearing at four years. (After Van Fleet in Jour. Heredity.)

exposed prairies. The first-generation progeny of such a cross are sterile in the males, but the females, crossed back with tame bulls, give animals which are still highly variable but combine in various degrees the conformation of the beef breeds with the ruggedness of the buffalo. The flesh

also partakes somewhat of the character of buffalo flesh, which was so highly prized by the native Indian and early plainsman.

Domesticated forms having a simple origin.—This outline of the origin of domesticated animals and plants includes only those forms which show clear evidence of having had a mixed beginning. Not all plants and animals have such a complicated ancestry. The pea and soy bean among plants and horses among animals, for example, have had a comparatively simple line of descent; yet they are represented by great variations in nearly every feature and are important additions to the list of cultivated and domesticated plants and animals.

Importance of hybridization.—The evidence is sufficient, however, to show that the one word which gives the key to the creation of useful forms of life is *hybridization*. The bringing together of qualities scattered about among different species, their rearrangement, and their higher development along strictly new lines—this is what hybridization makes possible; and while it is not the primary method of evolution it is the most rapid means of changing animals and plants under the controlling hand of man. When it is noted that the forms which have come into domestication within recent times, especially where rapid progress is made, are unmistakably the result of hybridization, it can not be doubted that germinal mixing in the past has been a most potent agency in the creation of valuable forms of life.

It is not without significance that the plants and animals, in both the Eastern and Western Hemispheres, which best serve the needs of man originated at or near the places where the great continents join. Southern Europe, Asia Minor, and northern Africa, in the Old World, have been the birthplaces of staple cereals such as wheat and barley. Cotton and alfalfa are other plants of great value indigenous to this region. The grape vine, date palm, fig, and olive are also native here. Sheep, swine, cattle, and horses were early used in these regions, as far as the evidence shows,

for the production of food and clothing and for carrying burdens. In the New World, maize, beans, long-staple cotton, the potato, sweet potato, tomato, squashes, and tobacco are the outstanding plant contributions, and all of them come from Central America or adjoining regions.

In each of the two hemispheres in which early civilizations developed, uninfluenced by each other, through long periods of time—the Egyptian and Assyrian in the East, and the Inca, Mayan, and Aztec in the West—we find the greatest progress in man's achievements made where the paths leading from continent to continent cross each other. During this period of upbuilding, use was undoubtedly made of the plants and animals nearest to hand. The fact that numerous forms of life, diversified by intermingling of different races from widely separated regions, were here most abundantly available furnished the best opportunity for the origin of domesticated animals and plants, and it is this fact which points the way for future progress.

CHAPTER XI

VIGOR ACCOMPANYING HYBRIDIZATION

SINCE the earliest times, animal husbandmen have been familiar with the fact that the crossing of different breeds or races of the same kind of farm animals tends to increase

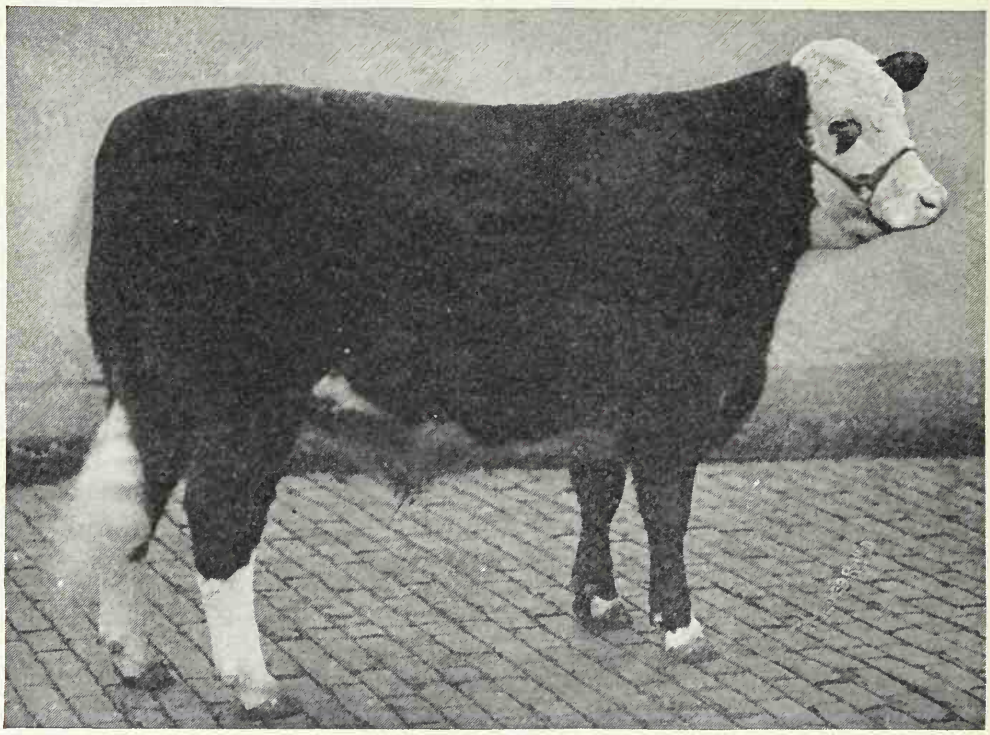


FIG. 115.—"California Favorite," a Hereford-Shorthorn cross that was the grand champion steer at the International Livestock Exposition, exhibited by the California Agricultural College. (After True.)

the size and sturdiness of the offspring. This effect, known generally as hybrid vigor, and technically as **heterosis,** is manifested in many different ways. The individuals immediately following a cross are frequently stronger, grow

larger, and mature in a shorter time than their parents. They are often notably resistant to unfavorable conditions.

Crossing among farm animals.—Hybrid vigor is a wide-

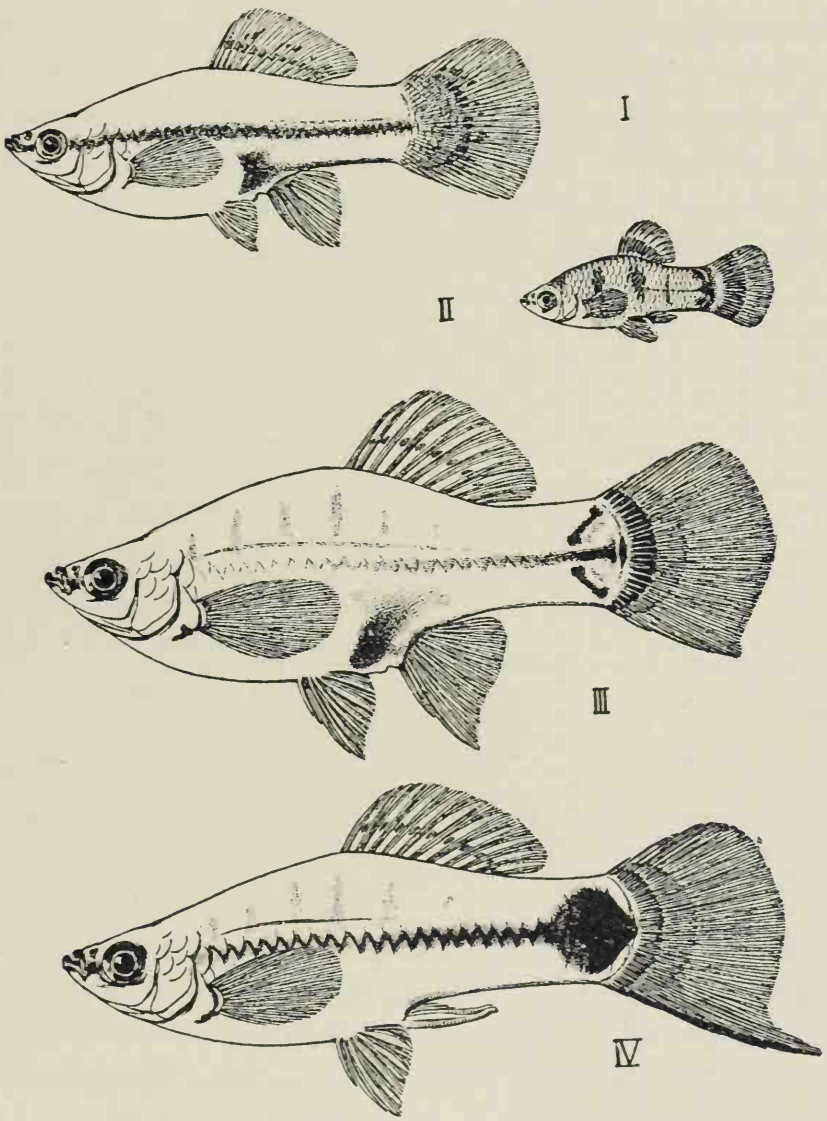


FIG. 116.—The result, in the first generation, of crossing different genera of fishes. I, *Xiphophorus strigatus*, female parent; II, *Platypoecilius maculatus*, male parent; III, female hybrid; IV, male hybrid. (After Gerschler in Zeitschrift f. Ind. Abst. u. Vererb.)

spread phenomenon shown by many animals and plants, both domesticated and in the wild. When the Chinese races of swine were introduced into England several hundred

years ago, it was a common practice to cross these with the native breeds to produce large, quick-growing animals for meat purposes, just as to-day the Poland–China and Chester–White crossbreds or Duroc–Jersey and Berkshire combinations are a familiar sight on many farms in the Corn Belt. The combination of Black Galloway or Aberdeen–Angus with a white Shorthorn makes an animal having a distinct color. These blue-gray, frosty-coated cattle of Scotland have long been known and esteemed for their large size, good form, and early marketability. The good quali-

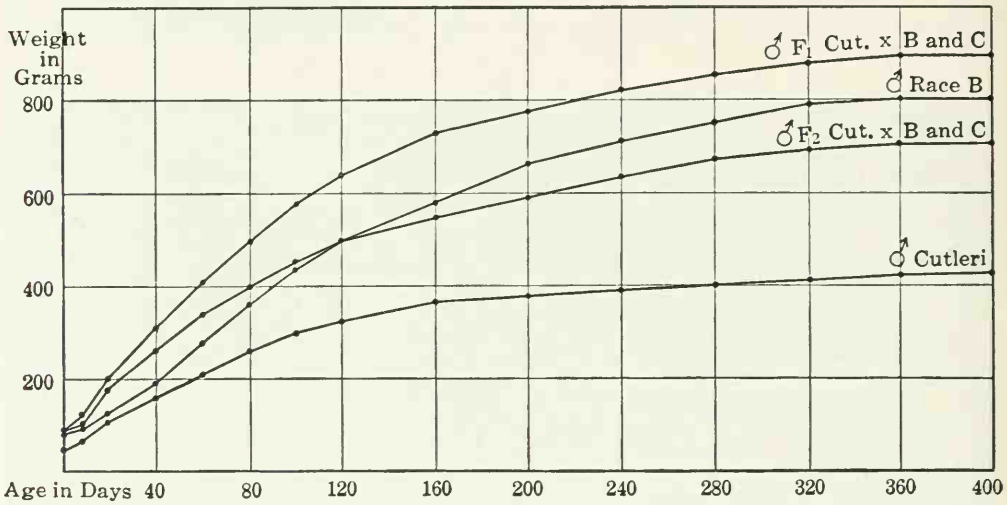


FIG. 117.—Growth curves of two different races of guinea pigs and their F_1 and F_2 hybrids. (After Castle and Wright in Carnegie Institution Publication No. 241.)

ties of the mutton and wool types of sheep are commonly brought together by crossing. Shropshire–Merino, Southdown–Rambouillet, Cheviot–Merino, and other crossbreeds are deservedly popular on account of their fast growth and usefulness as producers of both meat and wool.

Hybrid vigor in other animals.—These are a few examples from the farm and range. Evidence from the experimental laboratories is no less abundant, and many forms of animal life have been tested. Among insects, silkworms show a noticeable amount of hybrid vigor, as do also the little fruit flies so useful for experimental purposes. Crosses between unrelated stocks of these insects, as a general rule,

result in greater viability of the eggs laid, earlier sexual activity, and longer life of the offspring.

At least in one case, two related species of fish have been crossed with a marked increase in size apparent in the hybrid offspring. Different races of guinea pigs, when united, give young which are heavier at birth than those of either pure race and which maintain their larger size throughout their life period, as shown in Fig. 117. The hybrid animals also reach sexual maturity earlier.

Hybrid mice proved superior in a test carried out by Miss Vicari. The cross was between rather closely inbred albino and Japanese waltzing mice. The reactions of the two parent races and the hybrids to a maze test were obtained by using the device shown in Fig. 118. In carrying out the trials, the mice are placed at the entrance, and in order to reach the food in the back part of the box they have to follow a prescribed route. The ability of the animals to learn by experience is shown by the way they make repeated trials. The result was that 10 percent of the hybrid mice made more perfect trials than any individual in either parental race, and the average of the hybrids taken together was better than that of the parents. The first-generation animals were physically sturdier and more alert. The superiority of the hybrids is apparently not due to their greater physical vigor, because the parents differ in this respect but are alike in the number of perfect trials they make.

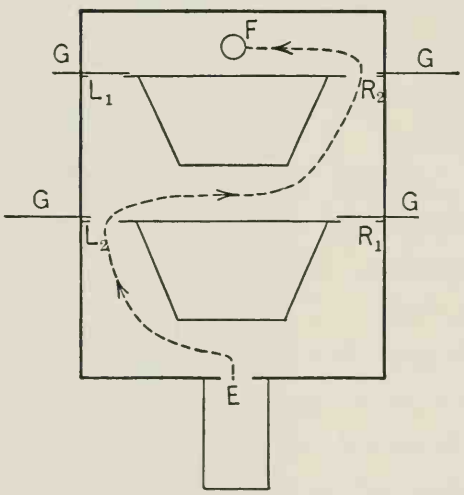


FIG. 118.—Maze used for testing hybrid mice. The right and left glass doors, R_1, R_2, L_1, L_2, through which the mice had to go to reach the food F, were opened in various combinations. Differences were found between the hybrids and their parents in ability to learn the correct route in repeated trials. (From the 1921 Report of the Carnegie Institution.)

Heterosis shown by plants.—The general biological importance of hybrid vigor is shown by the fact that it is exhibited among plants as well as animals. The first artificial plant hybrids to be systematically studied gave several remarkable instances of this stimulating effect. Kölreuter, in 1776, crossed many different species of tobacco and was astonished at the rapid growth and large size of the resulting plants. Naudin somewhat later made crosses among jimson weeds, and obtained hybrids which were twice as tall as either parent when grown under the same conditions. The same phenomenon has been clearly shown in some degree by many cultivated plants, such as peas, tomatoes, peppers, egg plants, cucumbers, squashes, and corn.

Vigor from species crosses.—Most of these examples represent combinations of different types within the same species, where the parental forms differ only in minor details. The same phenomenon is shown in even greater degree by many crosses between widely different groups. Usually hybrids between well-recognized species can be obtained only with difficulty, and in some cases the hybrid progeny are weak and sterile; but numerous species hybrids, although sterile, are remarkable for their size and sturdiness. The mule is a familiar example of a sterile cross between two radically different types. This combination of good qualities from two long-used races of draft animals has been known for fully four thousand years and is steadily growing in popularity in spite of its handicap of being valueless for breeding purposes. The mule is large and strong and has the advantage over the horse in that it can thrive under adverse conditions of care and feeding which would be unfavorable for its larger parent.

A similar cross of the ass and zebra has been tested and found to have several valuable qualities of possible future importance. The difficulty that stands in the way of the production of zebrules, as they are called, is that the zebra is not available in large enough numbers. The first

cross of our common cattle with the humped zebu from India has made a useful animal for Brazil, and for the southern parts of this country. This animal is a good meat producer, and at the same time is immune to certain diseases which prevent the profitable utilization of cattle in warm regions.

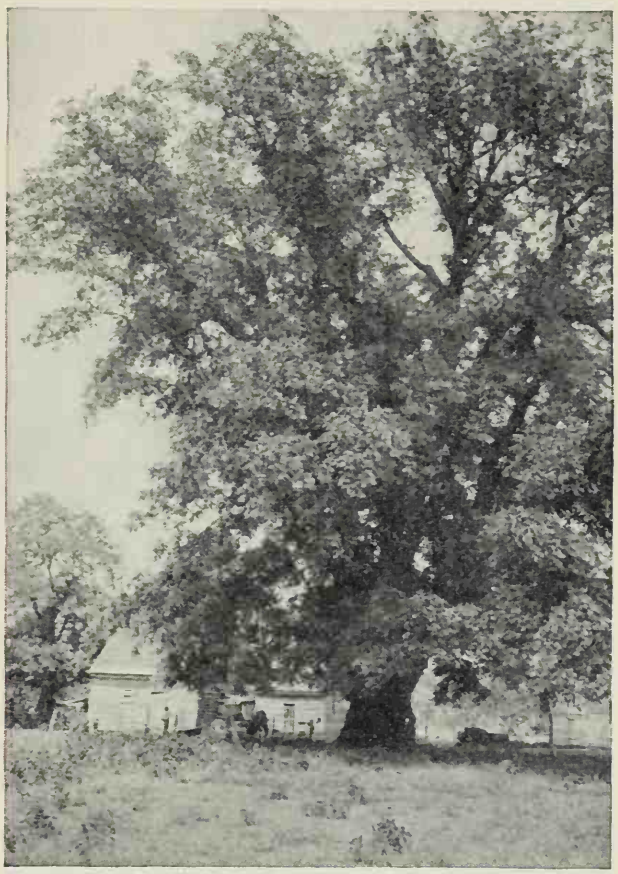


FIG. 119.—The James River Walnut. Considered to be a natural hybrid between the Persian Walnut and the native Butternut; height, 166 feet; spread of branches, 134 feet; circumference of trunk, 31 feet. (After Bisset in Jour. Heredity.)

Tree hybrids.—Numerous hybrid trees have attracted attention. The James River Walnut has been famous for some time on account of its large size and general robustness. This tree is considered upon good evidence to be a natural hybrid between the Persian Walnut and the common Butternut. A similar large and handsome tree, supposedly of the same ancestry, has been found growing

in New England and is remarkable in the fact that it is able to withstand the low temperatures of winter in a region in which the Persian Walnut is not able to survive. Walnuts seem to be notably induced by hybridization to greater growth. Burbank's Paradox Walnut is a first-generation

FIG. 120.—A hybrid poplar characterized by rapid growth, *Populus angulata* × *P. trichocarpa* twenty-seven months from seed. (After Henry in the Journal of the Dept. of Agricultural and Technical Instruction for Ireland.)

hybrid made by crossing the native California Walnut with the Persian variety of commerce. Another cross, called the Royal Walnut, is the combination of the native California with the eastern Black Walnut. These trees are also very vigorous, but, like all hybrids, they will not breed true, and since they can not be easily propagated vegetatively are hardly worthy of varietal names.

The Carolina Poplar, or Norway Poplar, as it is also called, is a rather recent introduction as a shade tree and thrives in nearly all parts of the country. It is an exceptionally rapid-growing tree with dark-green foliage. A valuable feature from a nurseryman's standpoint is the ease with which it can be propagated by cuttings. Its vigorous nature is thus easily maintained, while the trees are multiplied in numbers. The parentage of this hybrid is considered to be the Cottonwood of the western plains and the European Black Poplar. It was first known in Europe about 1700, when the first introductions of our native tree had been grown there long enough to flower. Augustine Henry, of Ireland, has tested many hybrid trees and finds that the poplars are notably stimulated by crossing, and that many other combinations deserve trial.

Teas' Hybrid Catalpa is an illustration of a natural

TABLE XXVII

COMPARISON OF THE FIRST GENERATION HYBRID OF CATALPA BIGNONIOIDES BY C. KAEMPFERI WITH ITS TWO PARENT SPECIES

	C. Bignonioides	C. Bignonioides × C. Kaempferi	C. Kaempferi
Bark	Rough	Smooth	Smooth
Leaf, upper surface	Glabrous	Pubescent	Pubescent
lower surface	Hirsute	Sparingly hirsute on young leaves	Glabrous
shape	Generally ovate	Generally cordate	Generally cordate
margin	Entire	Three-lobed, rarely entire	Three-lobed, rarely entire
Petiole	Slightly colored only on young leaves	Colored	Deeply colored
Insertion of petiole	Uncolored	Colored on young	Colored on all leaves
Notches in veins	Uncolored	Uncolored [leaves]	Colored
Flower, color	White with brownish-purplish spots and orange stripes	White with brownish-purplish spots and orange stripes	Pale yellow with brownish-purplish spots and dark yellow stripes
length	3 to 3.5 cm.	3–3.5 cm.	2 cm.
breadth	3 to 3.5 cm.	2.5–3 cm.	2 cm.
Pods, length	30 to 35 cm.	20 to 40 cm.	20 to 30 cm.
breadth	1 to 1.5 cm.	.5 to 1 cm.	.3 to .5 cm.
Seeds, length	2 to 2.5 cm.	2. cm.	1 cm.
width	.7 to .8 cm.	.3 to .4 cm.	.2 to .3 cm.
hair length	2 cm.	1.5 to 2 cm.	.7 to .8 cm.

hybrid which has since been reproduced by artificial crossing of two known species. The original tree was found growing among several kinds of Catalpas in a nursery, and from its appearance it was judged to be the product of the native *Catalpa bignonioides* with the Japanese *C. Kaempferi.* Later, these two species were artificially united by controlled pollination and the hybrid agreed closely with the description

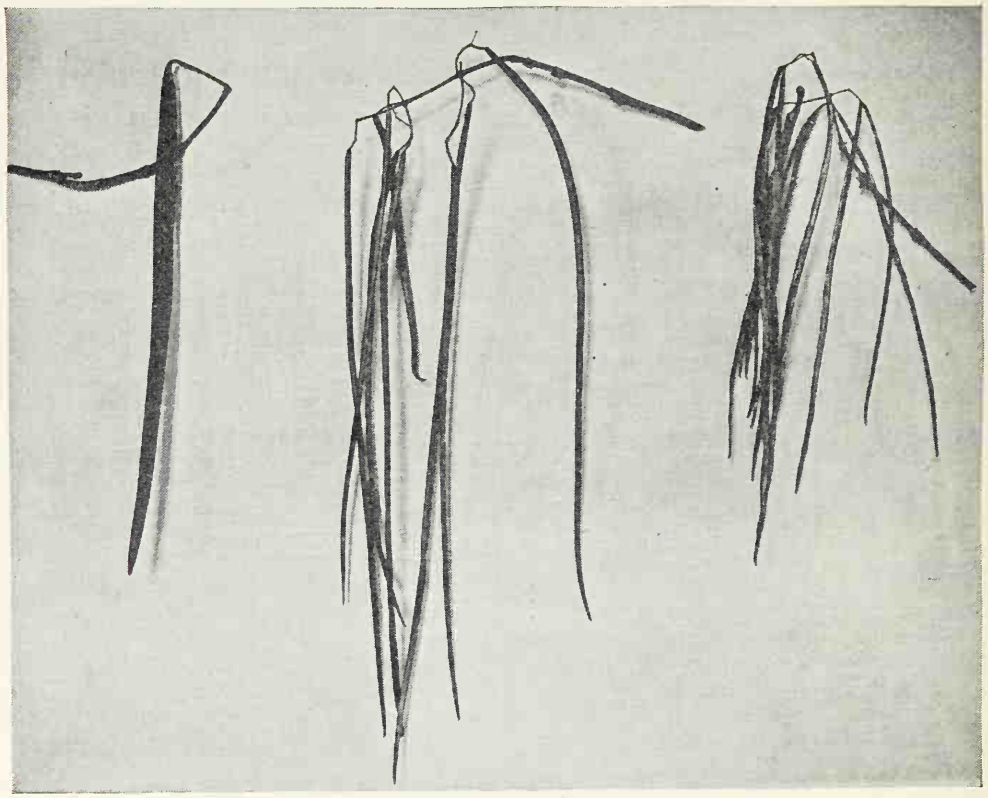


FIG. 121.—Mature inflorescences of *Catalpa bignonioides* (left) and *C. Kaempferi* (right) and the first-generation hybrid between these two species in the center.

of the original trees. As shown in Table XXVII the characteristic features of both parents were expressed in their hybrid progeny in varying degrees. After seven years of growth, the cross averaged 13 feet in height, compared with 11 feet for the native parent and 9 feet for the Japanese species. Diameter of trunk and spread of top were proportionally larger. The hybrid trees flowered profusely, and the total production of seed was several times greater

than for either parent. These were the results from trees grown in southern Connecticut. The same hybrid grown farther north showed up to much better advantage, because in that location the larger-growing parental race was killed to the ground every winter and grew out again each summer into a mass of shrubby sprouts. The small-growing Japanese species and the hybrid were not injured. The hardiness of one parent combined with the larger size of the other parent, together with other favorable growth factors contributed by both, made possible a tree which excelled both parents in a very striking manner.

Manifestations of hybrid vigor.—From these specific examples of crossing, which resulted in greater vegetative luxuriance and increased reproductive ability, it is seen that hybrid vigor finds expression in many different ways. Along with increments in size, there is frequently shown a hastening of the time of flowering and maturing. The investigations of Kölreuter, Gärtner, Focke, and Darwin show a large number of crosses wherein the hybrid flowers before either of the parents. Both Kölreuter and Gärtner give instances of perennials which commonly bloom in the second or third year and whose hybrids bloom the first year. The most extensive observations bearing on this relation of heterosis to time of flowering are those of Darwin, reported in his "Cross and Self-Fertilization in the Vegetable Kingdom." He gives the time of flowering of 28 crosses, between different varieties within many different species, which show positive evidence of hybrid vigor. Of these, 81 percent began to flower before the parents.

Hastening of maturity.—In a comparison of first-generation tomato crosses over a period of four years at the Connecticut Station, it was found that Stone×Dwarf Champion yielded on the average 16 percent more than the larger-bearing parental variety and at the same time ripened its fruit as early as Dwarf Champion. The difference in time of ripening the first fruits and in the average time of production of the whole crop of the two varieties was

not large, but the consistent earliness of the hybrid in the four years tested is significant.

A large series of crosses among inbred strains of corn has shown that the time of flowering and maturing, in this plant of definitely determinate type of growth, is perceptibly advanced. The hybrid plants not only produce a greater total amount of growth but do this in a shorter time, which demonstrates their greater rapidity in carrying on their life processes. Animal crosses which exhibit hybrid vigor may likewise show a shortening of the time required to reach sexual maturity, as illustrated by guinea pigs.

Plants with an indeterminate type of growth may not be earlier in flowering, although this is the case with the tomato, but may, on the other hand, be so stimulated to vegetative growth that seed production is delayed or even entirely prevented. This is true of some wide crosses, such as the combination of radish and cabbage. In this peculiar plant, so many diverse elements are brought together that seed production is impossible and all the energy of the plant is expended in an excessive and uncontrolled vegetative growth. See Fig. 162, page 381.

Increased longevity.—Plants which differ in their length of life usually give to their hybrid offspring a longevity equal to, if not greater than, that of the longer-lived parent. Gärtner notes especially that the crosses of annual herbaceous species with perennial shrubby species (as illustrated by the genera: *Hyoscyamus, Nicotiana, Calceolaria, Malva,* and *Digitalis*) are as enduring as the perennial parent. Pearl gives a very clear demonstration of the longer average life span of hybrid fruit flies as contrasted with their parents. His results are shown in Fig. 122. We must conclude, therefore, that crossing in both animals and plants not only hastens sexual maturity but also lengthens the period in which life exists in the organism.

Greater hardiness.—Ability to withstand low temperatures which damage their parents is another manifestation

of hybrids. Along with the catalpa and walnut illustrations already given numerous instances of this effect are listed by the earlier hybridizers. Kölreuter, Gärtner, Wiegmann, and Sageret, to whom we are indebted for an extensive knowledge of the behavior of hybrid plants, all described crosses in *Lycium, Nicotiana, Rhododendron* and *Lobelia* which could be grown in the open, one or both of whose parent races had to be wintered over in the green-

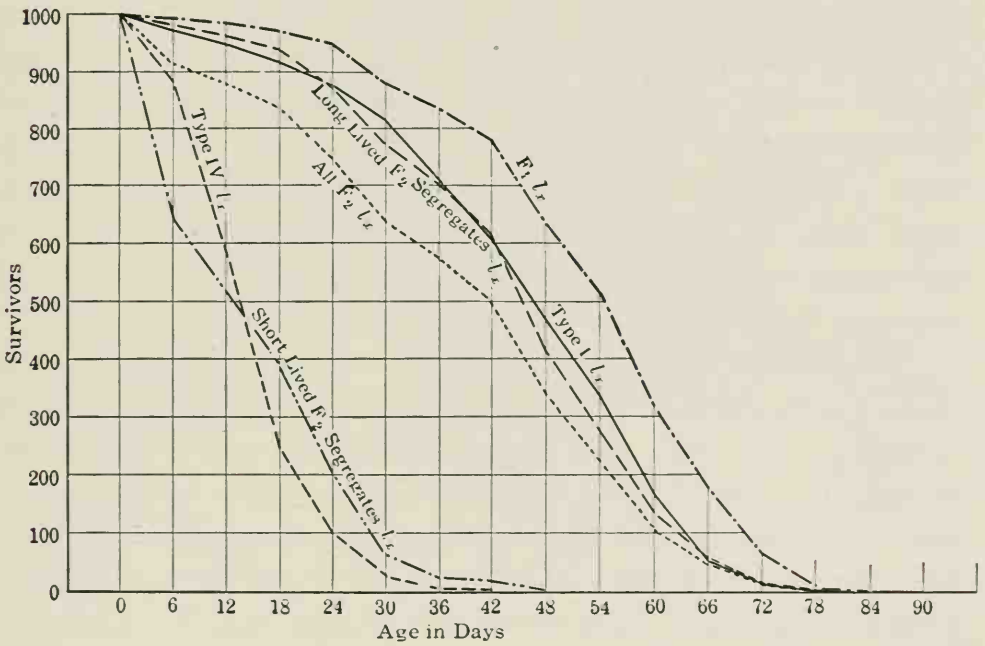


FIG. 122.—Graphs showing the survivors at different ages of a short-lived and long-lived strain of *Drosophila* and their F_1 and F_2 hybrids. After Pearl in Science Monthly.

house or cold frame. Increased winter hardiness, equaling or surpassing that of the more hardy parent, is not universally found but is certainly a common result.

Better viability.—Seeds of corn show a notably increased ability to germinate, as a result of crossing. A series of comparisons was made by obtaining self-pollinated and cross-pollinated seeds upon the same ears, the crossed seeds being distinguished by difference in color. Ripened under the same conditions, the two classes of self-fertilized and

cross-fertilized seed were strictly comparable and gave a difference of 16 percent better germination on the part of the crossbred seeds.

Augmented facility of vegetative propagation.—Hybrid plants are sometimes noted for their facility of vegetative propagation, even when there is no other indication of hybrid vigor. Many plants in the wild have largely given up reproduction by seed and depend upon some method of vegetative division, such as runners, layers, and underground root stocks, for their multiplication and dispersal. Familiar examples are strawberries, bramble berries, and many weeds and grasses. Undoubtedly many of these plants owe their vegetative luxuriance in part to hybridization. This asexual method of reproduction has the advantage that it maintains the hybrid combination and its accompanying vigor intact, which is not the case when reproduction takes place by seed.

Resistance to disease and insect injury has been noted in a few cases, but is not as general as the other effects of crossing. In corn, the union of strains which are badly attacked by smut with those which are little injured gives the hybrid nearly the same resistance as the immune parent. On the other hand, Weston finds that downy mildew attacks corn and corn-teosinte hybrids readily, although teosinte is immune. On the other hand, Gernert noted that a similar cross was not damaged by aphis which severely injured corn growing under the same conditions.

Heterosis due to differences in germinal constitution.—Darwin was greatly interested in the effects of inbreeding and crossbreeding because of the bearing these had upon the evolution of animals and plants. He found that it was the bringing together of diverse elements from compatible but somewhat unrelated types, and not the mere act of crossing, which resulted in the greater growth. Pollinations made between different flowers on the same plant, or between different individuals of the same ancestry, brought about no change. It was when unlike varieties native to different

regions were united that the most noticeable results were secured.

This is well shown by a series of crosses in corn. When different varieties of the same type, growing in the same region, are combined, there is usually not much increase in production of grain. When different types, such as flint and dent varieties, are crossbred, the beneficial effects are

FIG. 123.—Two cultivated varieties of Rhododendron and their first-generation hybrid. (After Hurst in Jour. Royal Hort. Society.)

more apparent. For example, in numerous tests carried out in Connecticut, it was found that, out of 50 crosses, 66 percent exceeded the more productive parent and 88 percent did better than the mean of the two parents. The average increase of all crosses compared with both parental varieties was 9 percent. Collins crossed several native Indian varieties of corn, grown in the Southwest, with introductions from China and got remarkable increases in yield.

Varieties known as Hopi, Hairy Mexican, and Brownsville corn, crossed by Chinese varieties, gave increases ranging from 100 to 126 percent above the average of the parental production.

The important fact is that types from different regions usually differ in many ways in their germinal make-up. Difference in appearance is an indication of such inherent unlikeness. The mere fact of previous residence in diverse

FIG. 124.—Reciprocal crosses between two varieties of tomatoes, each of which possesses a dominant factor lacking in the other. The hybrid plants in the center have normal foliage and tall stature and are unlike either parent.

regions is of no significance unless there are also hereditary differences. Crossing among plants of the same strain of tobacco which had been grown separately for a long period in Italy and in this country gave no indications of hybrid vigor. But two different varieties, one of which had originally come from Italy and had been grown for a number of years in this country along with the other, when crossed by East, gave a noticeable increase in size.

Explanation of hybrid vigor.—From the illustrations given it is evident that there is a tendency for the features

of both parents to be expressed in the offspring. This is the basis for an understanding of the vigor derived from crossing. There are a greater number of different hereditary factors in a hybrid individual than in either pure parent. Nearly all variations that are recessive are less favorable to the development of the organism than their dominant mates. Examples have already been given in the chapter on the chromosomes, "the carriers of the inheritance." Since crossing brings out those qualities which help the individual in its growth and suppresses the abnormal and unfavorable characters, it is to be expected that hybrids will tend to be strong and vigorous. This will be true, however, only if each parent is able to supply the deficiency of the other, and if the forms crossed are not so diverse that their union is incompatible with normal growth. If the parents are themselves hybrids, further crossing may bring together no greater number of dominant favorable growth factors but may even uncover recessive characters. Hence, further crossing can not usually increase size and vigor, and in fact may even result in the appearance of weaknesses. This is clearly understandable from the operation of Mendel's principles of heredity.

As noted before, the product of the union of a dwarf type of corn with a golden variety gives tall, vigorous, and healthy green offspring. But if such a normal plant is pollinated by another hybrid plant, which also carries the same recessive weaknesses, golden plants and dwarfs will reappear. These are striking examples of clearly undesirable characters. Such are relatively few in number, but they show the way in which crossing operates to bring about a greater growth than the parents are able to obtain, and why further crossing may not be able to continue to produce this result. By far the larger number of factors which control the development of the organism are less easily identified than dwarfness and chlorophyll deficiencies; but all factors work together to a greater or less extent and in the same way bring about the beneficial

results associated with hybridization and the directly reversed effects of inbreeding.

A theoretical illustration of heterosis.—This hypothesis may be made clearer by a concrete diagrammatic illustration. A case will be assumed in which two homozygous

FIG. 125.—The result of crossing a golden variety of corn lacking normal chlorophyll (right) with a dwarf variety (left). The first-generation hybrid plants are all tall and dark green.

individuals, having 3 chromosome pairs, both attain the same development, as represented by any measurable character. This development will be considered to amount to 6 units, 2 of which are contributed by each chromosome pair. One of these individuals, which we will call X, attains its development through the operation of factors distributed in the 3 pairs of chromosomes, each dif-

fering from the others in its contribution. Any number of factors may be chosen, but, for the sake of simplicity, only 3 in each chromosome will be employed. These are numbered 1, 3, 5; 7, 9, 11; and 13, 15, 17 in the accompanying diagram (Fig. 126). The second individual, *Y*, develops to an equal extent in the characters measured. It

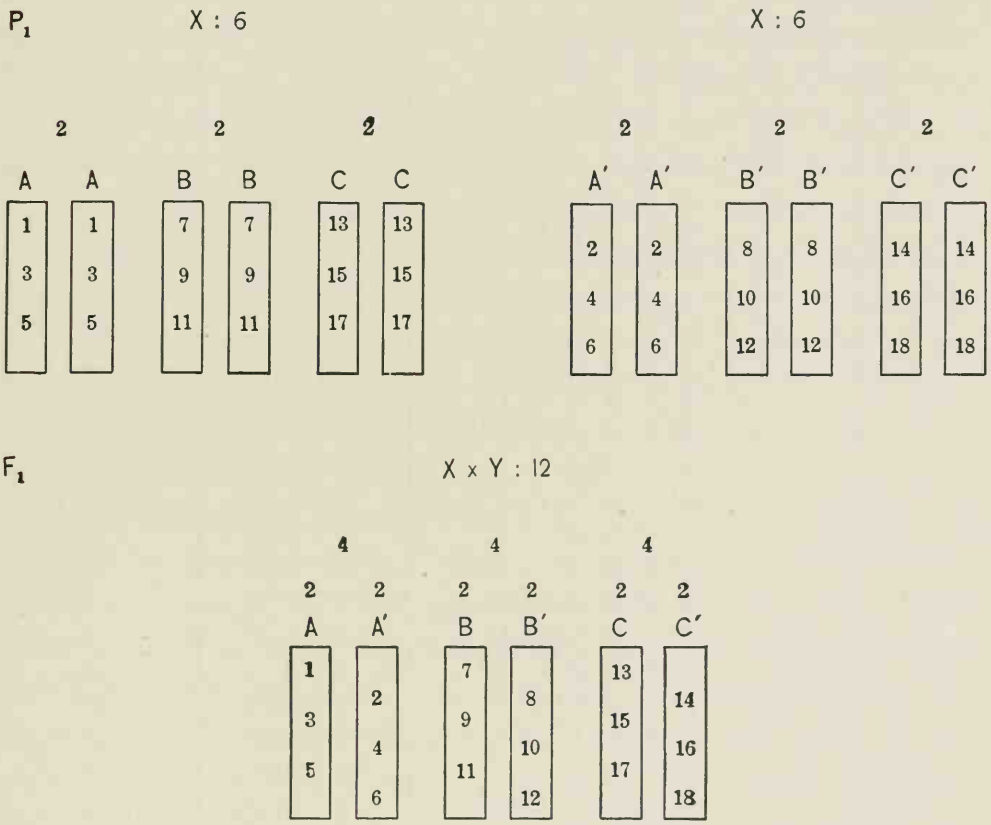


FIG. 126.—To show how dominant factors contributed by each parent may enable the first generation of a cross to obtain a greater development than either parent.

attains this same development, however, by the operation of a different set of dominant factors distributed in the 3 chromosomes and numbered 2, 4, 6; 8, 10, 12; and 14, 16, 18 in the diagram. Both individuals are homozygous; i.e., the allelomorphic pairs are composed of like elements. The recessive factors in one individual, which are allelomorphic to the dominant factors in the other, are not shown. It is also assumed that all these 9 factors are as fully effective

TABLE XXVIII

COMPOSITION OF A TRI-HYBRID POPULATION IN F_2 AND THE DEVELOPMENT WHICH EACH INDIVIDUAL ATTAINS, DEPENDING UPON THE TOTAL NUMBER OF DIFFERENT DOMINANT FACTORS PRESENT

Number of Individuals in Each Class	Class	Contribution of Each Chromosome Pair	Total Development
1	A A B B C C	2+2+2	6
2	A A′ B B C C	4+2+2	8
2	A A B B′ C C	2+4+2	8
2	A A B B C C′	2+2+4	8
4	A A′ B B′ C C	4+4+2	10
4	A A B B′ C C′	2+4+4	10
4	A A′ B B C C′	4+2+4	10
8	A A′ B B′ C C′	4+4+4	12
1	A A B B C′ C′	2+2+2	6
2	A A B B′ C′ C′	2+4+2	8
2	A A′ B B C′ C′	4+2+2	8
4	A A′ B B′ C′ C′	4+4+2	10
1	A A B′ B′ C C	2+2+2	6
2	A A B′ B′ C C′	2+2+4	8
2	A A′ B′ B′ C C	4+2+2	8
4	A A′ B′ B′ C C′	4+2+4	10
1	A′ A′ B B C C	2+2+2	6
2	A′ A′ B B′ C C	2+4+2	8
2	A′ A′ B B C C′	2+2+4	8
4	A′ A′ B B′ C C′	2+4+4	10
1	A′ A′ B′ B′ C C	2+2+2	6
2	A′ A′ B′ B′ C C′	2+2+4	8
1	A′ A′ B B C′ C′	2+2+2	6
2	A′ A′ B B′ C′ C′	2+4+2	8
1	A A B′ B′ C′ C′	2+2+2	6
2	A A′ B′ B′ C′ C′	4+2+2	8
1	A′ A′ B′ B′ C′ C′	2+2+2	6
64 Total			

DISTRIBUTION OF THE F_2 INDIVIDUALS ACCORDING TO THE DEVELOPMENT ATTAINED

Classes.....	6	8	10	12	= 4	Number of classes
Frequencies.....	8	24	24	8	=64	Number of individuals

in the haploid as in the diploid condition; in other words, they show perfect dominance over their absence. It will be seen from the diagram that when these individuals are crossed together, the progeny develop to twice the extent of either parent, because there are present 18 different dominant factors instead of 9.

Following this hypothetical case into the second generation by selfing or by interbreeding the individuals of the first generation, the data given in Table XXVIII are obtained. Summing up the results of this tabulation, it will be found that 8 individuals are completely homozygous and reach the same development as either parent, 6 units; 8 are heterozygous in all 3 chromosome pairs and duplicate the 12-unit growth of the first generation; the remaining 48 individuals fall into equal-sized groups, developing to 8 and 10 units, respectively. In other words, the distribution is symmetrical, and this symmetry remains, whatever the number of chromosomes involved.

It should also be noted that the mean development of the second generation is 9 units, which is an excess of just half the excess of the first generation over the parents. The extra growth derived by crossing the two different types has diminished 50 per cent. In the third generation, from a representative sample of the second generation, it can be shown that this excess again diminishes 50 percent, so that the effect on the average is only 25 percent as great in this generation as in the first, and so on, in subsequent generations, until the effect diminishes to a negligible quantity in about the eighth generation. This is in fair agreement with the actual results obtained by inbreeding maize.

Objections to the dominance hypothesis.—It was formerly held that dominance of favorable factors could not be an adequate means of accounting for hybrid vigor, because with dominance alone there would be an asymmetrical distribution in F_2 whenever heterosis was exhibited in F_1. Moreover, it was thought that all the dominant factors could be recombined in the homozygous condition so as to

give individuals that would not be reduced by inbreeding. When linkage is taken into consideration, neither of these objections holds. Collins has also pointed out that even without linkage the asymmetry in F_2, with a large number of factors involved, would not be noticeable, and the difficulty of recombining a large number of independent factors is so great as to render homozygous combinations of all the most favorable characters very unlikely.

Perfect dominance not the rule.—In the preceding illustration of the way in which heterosis may be brought about, perfect dominance was assumed. Moreover, breaks in linkage with the formation of new linkage groups were not considered. All these things enter as complicating factors. Perfect dominance, except in more or less superficial characters, rarely occurs, and even when it does occur, it may be merely an appearance rather than a reality. The general consensus of opinion at the present time is that there is no such thing as perfect dominance, that the heterozygote merely approaches the condition of one or the other parent more or less closely. When two different potentialities are contributed by the parents, there results an interaction between them and the end product is represented in the organism. Because the most striking effect may resemble the character of one parent more than the other, we say that this character is dominant. In reality, in the more fundamental characters, the hybrid usually shows a resemblance to both parents. The more common illustrations of dominance, such as fur and flower colors, probably have little to do with heterosis. Other dominant characters, however, have a fundamental effect upon development, nearly always being essential to greatest vigor. Various grades of albinism are common in maize and in many other plants. Since this affects the amount of chlorophyll, the presence of albinism in any form seriously retards growth. In extreme cases, the plants are totally incapable of continuing existence beyond the stage made possible by food stored in the seed. In animals, albinism does not have the

physiological significance that it has in plants, but even here it is sometimes unfavorable to the individuals showing it. In every case and in all degrees, true albinism is recessive to the normal condition. In maize, the heterozygous green plants can not be distinguished from homozygous green plants. Many other unfavorable characters in maize are also recessive. Absence of brace roots, bifurcated ears, dwarfism, and susceptibility to smut, all behave in this way.

Recessive factors cumulative in their effect.—Of the more than one hundred and fifty mutations which have been described in Drosophila, the great majority are recessive and practically all of them are less favorable to the development of the fly than the wild-type characters. The effect of the recessive factors is cumulative, because when many of them are brought together the flies are extremely difficult to keep alive.

Since dominant variations are always expressed, all those which are detrimental to the organism are quickly eliminated by natural selection. However, if a dominant mutation proves favorable to the survival of the organism, individuals having the new characters will tend to supplant the old forms, and the new variations will quickly become the stock in trade of the species. On the other hand, recessive variations, being masked and carried along by crossing, are not so quickly eliminated. The way in which such hereditary weaknesses may persist is well illustrated in the white seedlings commonly seen in small numbers in nearly every corn field.

An actual illustration of dominance and linkage.—For an actual case showing how dominance and linkage work together, we must turn again to the work with Drosophila. There is an enormous amount of data from which to choose, but in order to have an example which is comparatively easy to follow, let us consider only four factor pairs which are located in the second chromosome. The principal effect of these factors gives them their name. They are long legs (*D*) dominant to " Dachs " legs (*d*), gray body (*B*) dominant

to black body (*b*), red eye (*P*) dominant to purple eye (*p*), and normal wings (*V*) dominant to vestigial wings (*v*). In gamete formation in the female, there are breaks with a frequency of 10 percent in the linkage between *d* and *b*, of 6 percent between *b* and *p*, and of 13 percent between *p* and *v*, disregarding some disturbing conditions which need not concern us here. In the male there are no linkage breaks.

Now, if a female fly with Dachs legs, gray body, purple eyes, and normal wings (*dBpV*) be crossed with a male having long legs, black body, red eyes, and vestigial wings (*DbPv*), the resulting progeny will have the usual wild-type characters, long legs, gray body, red eyes, and normal wings, and be considerably more vigorous than either parent. If these factors segregated independently, one would expect to find 1 gamete out of every 16 to be of the constitution *DBPV*, and to obtain 1 F_2 individual homozygous for this combination of the four dominants out of every 256. As a matter of fact, owing to the linkage relations existing, only 1 gamete of this kind is produced in 2000 and then only in the female. It is, therefore, impossible to obtain the type sought in the F_2 generation; but the males of the all-dominant type will appear in F_2, and the pure strain may be established in F_3. The word " may " is used as a sort of forlorn hope, however. There is a possibility of establishing the homozygous dominant strain in F_3, but when one realizes that in F_2 only 1 such male and 1 heterozygous female, similar in appearance to hundreds of her sisters, will be produced in every 4000 progeny, the difficulties in the situation are emphasized.

Difficulty of recombining homozygous dominants.— The frequency of the linkage breaks is large and the number of factors small in the illustration just given. When it is remembered that in other organisms there are 10, 20, or even 40 chromosome pairs to be considered, with possibly dozens of factor differences, instead of 4 in each chromosome, some idea may be obtained of the real difficulties

involved in producing individuals of maximum vigor unaffected by inbreeding. Practically speaking, it is impossible unless one is dealing with a small number of loosely linked factors, except when long periods of time are available and when natural elimination of undesirables is high.

FIG. 127.—Complementary color factors in guinea pigs, black and white, give the wild type, agouti.

Complementary factors.—Numerous instances are known in which factors by themselves are without effect, but function properly when associated with other factors. The wild-type coat pattern of many rodents is made up of color distributed on the hairs in such a way as to give an indistinct neutral shade. This ticked, or agouti, pattern has

been analyzed into one or more factors which produce the basic colors, and certain entirely different hereditary factors which govern the distribution of these colors on the hairs. Without the distributing factors, the animals are evenly colored black or brown as the case may be. The pattern factor itself, separated from the color factors, can produce no effect. Only when both are present are the animals protectively clothed. The seeds of maize owe their color in certain shades to a similar set of circumstances. In one case, three different basic factors and one modifying factor must be present to make the purple color familiar in many strains of native Indian corn. When any one of the three basic factors is lacking, no color is produced; without the modifying factor, the color is red.

These are illustrations of the manner in which complementary factors work together to produce a given result. The coat patterns of guinea pigs, rats, and mice and the colors of corn and other plants probably play no important part in hybrid vigor; yet they make plain in a very effective way a state of affairs which exists in more important functions of living organisms.

Summary.—From the foregoing it will be realized that if any individual is deficient and handicapped in its hereditary make-up, there is a good chance that its need will be supplied when it is crossed with other individuals, because all are not apt to be wanting in the same things. What one lacks is furnished by the other, and conversely. In other words, there is a pooling of hereditary resources, with the result that the combined effect is better than either could produce alone.

It should now be clear that the beneficial effects of crossing follow from the working of the laws of heredity and not from any mysterious stimulus from the act of crossing itself. If good qualities exist in the parents, but not in sufficient amount or not in their proper association, then there is a good opportunity for the offspring to bring together the favorable factors from both and surpass their

parents in development. This is a temporary and transitory effect, however. The increased vigor is shown at its maximum only in the first generation following the cross, and is quickly lost in later generations unless it can be perpetuated by some form of asexual reproduction.

CHAPTER XII

INBREEDING

ANIMAL husbandry has engaged the attention of man since earliest times and was brought to a high degree of perfection by the ancient Semitic tribes. It can not be doubted that the results of different systems of mating were noted and commented upon. The ill effects frequently following the inbreeding of livestock have probably been the basis for the widespread prejudice against this system of mating, a prejudice which has resulted in the customs and laws against the marriage of near kin.

Doubtless this opinion was not founded upon any carefully weighed evidence; in all likelihood it was nothing more than a rule-of-thumb adopted after casual observations. But so powerful is the force of general opinion that apparently no attempt was made to practice systematic inbreeding with animals until the eighteenth century.

First application of inbreeding to animals.—Robert Bakewell (1725–1795) was the pioneer in showing the value of close mating as a means of fixing a uniform type. His efforts were directed mainly to the breeding of sheep, although he gave some attention to Longhorn cattle and Shire horses. His principal work was that of founding the Leicester breed of sheep and bringing them to a high degree of perfection. Bakewell's practice of mating brother with sister and parent with offspring horrified his neighbors at first; but they soon appreciated the practical results he secured, because the yearly revenue from the services of his rams rose from about $4 to $2000 in thirty years.

The period of Bakewell's activity was that of the beginning of the rise to popularity and fame of many of the

standard beef breeds of England, as we know them to-day. At that time the Herefords and Shorthorns first took on recognized forms and distinguishing color patterns. Throughout their early history there is frequent reference to Bakewell and his system of intensive breeding. It was the mating of like with like, relative with relative, individuals which showed the highest expression of desired characters with others belonging to the same ancestry, that brought about fixity of type, increased the ability to transmit their good qualities, and made it possible for progeny of uniform excellence to be regularly produced. It was not until inbreeding was systematically practiced that the breeds of cattle, horses, sheep, and swine began to take on the forms and patterns which are now familiar to us.

Difference of opinion regarding inbreeding.—Among animal breeders at the present time there is still a great variety of opinion in regard to the effectiveness and limitations of the practice of inbreeding. There are those who stoutly maintain that inbreeding rightly practiced is never injurious. Others hold that it is always harmful in greater or less degree. Most breeders stand in a middle position, saying that the results are sometimes good and sometimes bad, depending on the stock worked with, the intensity of the inbreeding process, the skill used in bringing together the right individuals, and other factors unknown. There is still much uncertainty in regard to this fundamentally important subject. One reads the conflicting opinions of livestock breeders without arriving at any satisfactory understanding of the principles underlying inbreeding.

The uncertainty is due to the fact that practical breeders are judging solely from their experiences with different families belonging to various breeds. Their observations must necessarily be limited. It is not possible to form any reliable judgment in regard to the workings of inbreeding until the mechanism of heredity is understood, and until carefully controlled experiments with animals and plants have demonstrated the truth of the laws governing the

transmission of inherited characters. One could cite many instances of famous animals which have resulted from a rigid system of inbreeding. Others equally prominent have come from a line that was very little inbred. In many cases inbreeding has clearly resulted in reduced size, loss of vigor, the production of abnormalities and monstrosities, and general disaster.

Nothing is to be gained by a further recital of these well-known facts. What is needed is an understanding of the underlying principles. These have been worked out only recently and are the result of experimentation and the correlation of all the facts from all fields of biological investigation.

Controlled experiments on inbreeding with animals.— Because of their length of life, the domestic animals are not suitable material for an extensive experiment on inbreeding. The smaller, rapid-breeding animals, such as rats, mice, and guinea pigs, are much better material for an investigation of this kind, where large numbers must be worked with over a period of generations, under external conditions which are approximately the same for all. In the past fifty years several extensive experiments with rats and mice have been carried out. Crampe and Ritzema-Bos, in Europe, bred rats by various systems of inbreeding. They found that there was a gradual decrease in size of litter and a gradual increase in the number of infertile matings. In one case the inbred rats manifested great susceptibility to disease and showed diverse kinds of abnormalities.

The reduction in fertility is given by Ritzema-Bos as follows:

Year of inbreeding	1	2	3	4	5	6
Average number in litter	7.5	7.1	7.1	6.5	4.2	3.2
Percent infertile matings	0.0	2.6	5.6	17.4	50.0	41.2

Crampe's results were similar to these. Both their experiments were started with albino females which had been outcrossed, one with a white and gray male, the other with a

wild Norway male. This complicates the analysis of the results, as there is an opportunity for Mendelian recombination. Factors for sterility and weakness could have existed in both parental races without being apparent. When the separate races were crossed and then inbred, these abnormalities would segregate out. Therefore, these experiments are not wholly satisfactory in showing whether or not inbreeding is injurious. To determine this it is necessary to start with a uniform stock that is fairly homogeneous in its genetic constitution. With such material it is possible to determine the effect of extended close mating without confusion as to the conclusions to be drawn.

Inbred mice.—Weismann inbred a stock of white mice for twenty-nine generations. The origin of these mice and the system of mating followed are not given. The average number of young obtained in three successive ten-generation periods were 6.1, 5.6, and 4.2. The average number of litters raised in the first part of the experiment was 22; in the latter part only 3. There was a greater opportunity to select healthy breeding stock in the earlier periods, which might account for a part of the marked reduction in fertility. Another investigator, Von Guaita, crossed some of these inbred mice with Japanese waltzers and found the average number of young in successive generations to be 4.4, 3.0, 3.8, 4.3, 3.2, and 2.3. This is a still further reduction in fertility, brought about possibly by recombination and segregation.

Wistar Institute's experiments with rats.—From the standpoint of numbers employed and the careful way in which a system of close mating was followed, none of the foregoing experiments can be compared with two extensive investigations which have been carried out recently with rats and guinea pigs. King, at the Wistar Institute in Philadelphia, started with a litter of four slightly undersized, but otherwise normal albino Norway rats, two males and two females. These were inbred by continued brother and sister mating. Two separate lines were carried along.

In the early part of the experiment, nearly all of the females were used for breeding, but after the sixth generation about twenty females were selected from approximately a thousand available young.

During the first six generations the rats exhibited many of the defects reported by previous investigators. The litters were small and many females were sterile. Other animals showed low vitality, dwarfing, and malformations. Similar

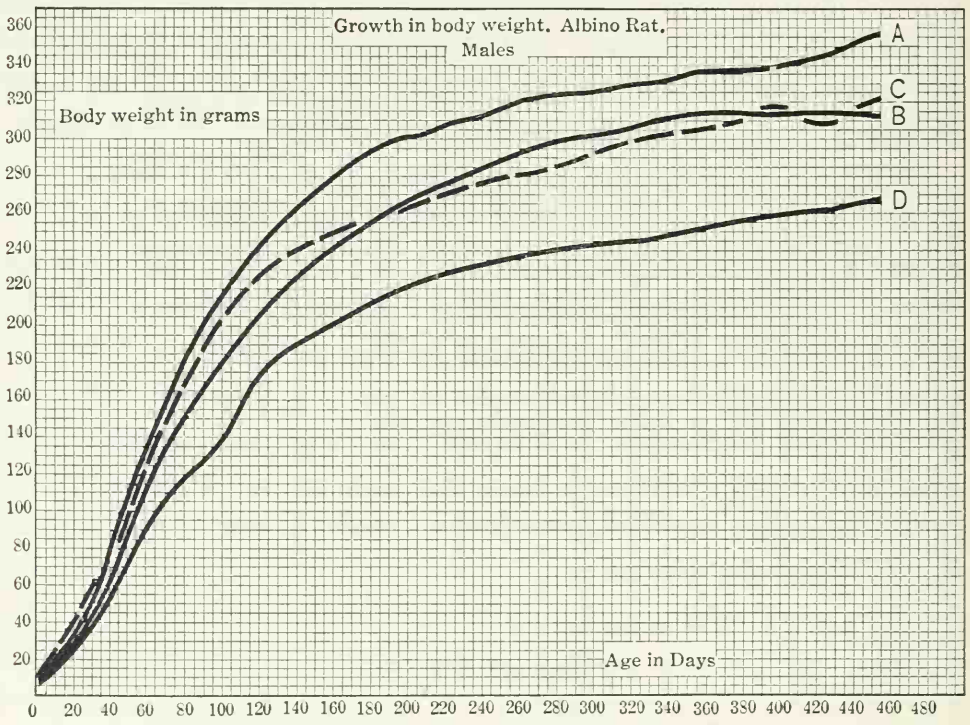


FIG. 128.—Graph showing the increase in weight of body with age for male albino rats; *A* and *B* represent two series of inbred rats, *C* and *D* are non-inbred controls. (After King in Jour. Exper. Zool.)

changes were being shown by stock rats, however, which were not inbred. This led to a radical change of food, following which these unfavorable results disappeared. Whether this improvement was due entirely to better food or may be attributed in part to segregating out of unfavorable factors and the selective elimination of weaker rats can not be fully determined. King gives greater weight to the food supply, and this is the most plausible explanation since the experiments were started with stock rats which

had already been rather closely inbred and therefore in approximately a homozygous condition.

Rats inbred for twenty-five generations.—After the change in food, and from the sixth generation on, there was a complete return to the normal condition in size and fertility, and this was held throughout the experiment which covered twenty-five generations. The body weight of the

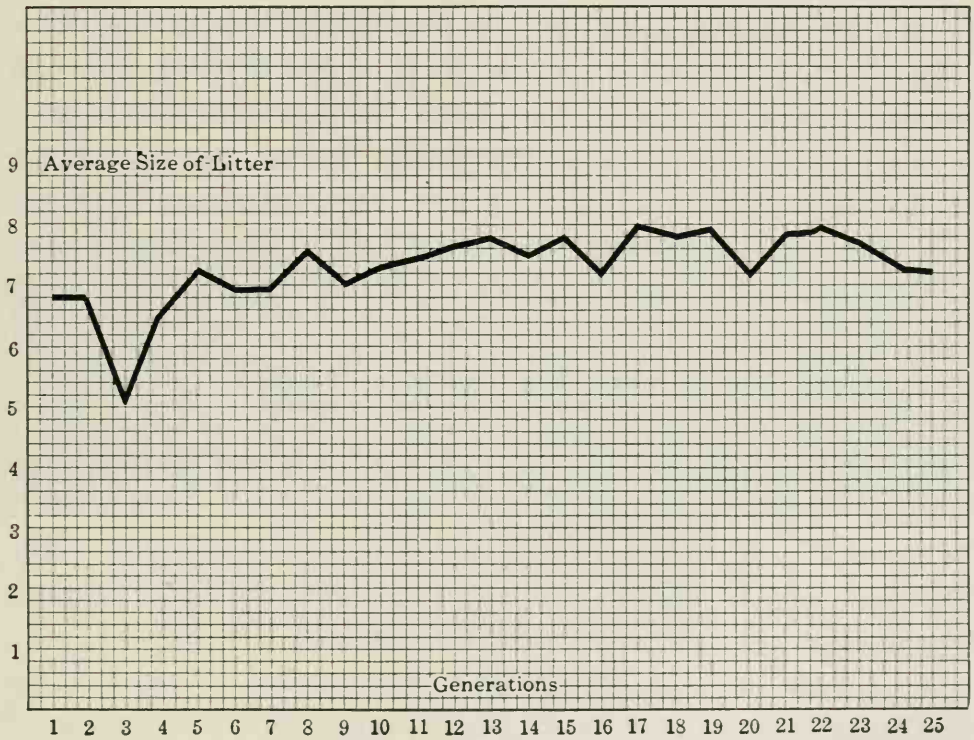


FIG. 129.—Graph showing the average size of litter produced in successive generations of inbred rats. (After King in Jour. Exper. Zool.)

inbred animals throughout their growth period is compared with stock animals, raised under similar conditions, but not inbred, in Fig. 128. The line *A* gives the growth curve of the inbreds during the seventh to the fifteenth generations. The line *C* is the curve for the stock rats during the same period. The lines *B* and *D* represent inbreds and stock rats during later generations.

No reduction in size and reproductive ability.—The results obtained for body weight were paralleled by those

for fertility and constitutional vigor as indicated by longevity. Neither was reduced by inbreeding; in fact there was a slight increase. Fig. 129 shows the average size of litter throughout the experiment. Some fluctuation is shown, as would be expected, but after twenty-five generations of the closest kind of inbreeding possible with bisexual animals, the fertility is no less at the end than it was at the start.

Differences in the two inbred lines.—The separately bred lines differed somewhat at the close of the experiment. The rats of one line were slightly more fertile, attained sexual maturity earlier, and lived longer than the others. There was a reduction in variability in both lines. Mendelian segregation had taken place. By selection, vigorous, uniform strains, which were somewhat larger, more fertile, and longer lived than many strains of stock rats, were built up.

The United States Department of Agriculture experiments with guinea pigs.—Another carefully conducted experiment with guinea pigs gave a somewhat different result. This investigation was begun by G. M. Rommel of the United States Department of Agriculture, in 1906. Later it was in charge of Sewall Wright, who has made a thorough analysis of the results obtained.

As with the rats, inbreeding was carried on exclusively by brother and sister mating. The experiment was started with thirty-three pairs of stock animals, which had been more or less closely inbred previously; and sixteen of these families were alive at the close of 1917, after some twenty generations of the closest inbreeding. Considering all the animals together, there was a decline in every character connected with vigor. The litters became smaller and were produced more irregularly. The mortality, both before birth and before weaning, was increased. However, there are now pronounced differences between various families. Some are still quite strong, comparing favorably with the original stock after twenty successive matings of brother and sister. Others lost vigor so rapidly that they

soon failed to reproduce, although every effort was made to continue them. Taking all qualities together, none of the inbred animals were as good as at the start; but among the surviving families many have certain particular qualities better developed than the average of the race. One family was greatly reduced in vitality, but not in size of body or number of young produced. In another, just the reverse situation ruled. Many different combinations of characteristics, some favorable and some not, were exhibited by the different families after a few generations of brother and sister mating. All the inbreds are noticeably more uniform. Altogether, more than 26,000 guinea pigs have

FIG. 130.—Four generations of inbred guinea pigs, after 16, 17, 18, and 19 successive brother and sister matings. The smaller size of the last pair at the right is due to their lesser age. (After Wright in U. S. Dept. Agr. Bull. 1090.)

been raised in this experiment, and their results, together with the preceding investigation with rats, represent the most extensive and reliable data on systematic inbreeding with animals.

Sterility reduced in Drosophila.—Fruit flies have been inbred by Castle and his students for fifty-nine generations, by brother and sister mating. At the close of this period, which would correspond to a century of cattle breeding, fertility was not reduced below the level for the race at the start. This experiment showed that inbreeding resulted in strains of unequal production of young. The less fertile tended to be eliminated, so that only the more fertile remained. Absolute sterility occurred frequently in the

first part of the experiment, but almost entirely disappeared in the later generations, as shown by the following figures:

Generations	Percent Matings Totally Sterile
6 to 24	17.80
25 to 42	18.47
43 to 59	3.37

Inbreeding experiments with domestic animals.—The above experiments were made with wild or semi-domesticated animals. Such animals are frequently forced to undergo more or less intensive inbreeding under natural conditions, and for that reason have been more vigorously selected and may not be expected to show the same results as farm animals. There is no case on record where such close mating has been practiced with the larger domesticated animals on such an extensive scale. Hays at the Delaware Station reports the results of inbreeding swine by brother and sister mating. The results were so unfavorable that they were not continued for more than a few generations.

Results with swine.—From a litter of a Yorkshire sow the best boar and sow were selected. These, bred together, produced a litter of twelve pigs, ten of which lived. A male and a female were again selected and gave birth to offspring from which one boar and three sows were selected. From this same pair a second litter of nine pigs was born the next year, but all except three of these died and the three failed to mature properly. The boar selected from the first litter failed to breed with his sisters and also with some Berkshire sows. When he was used with his dam there were produced six pigs, all of which were dead at birth or died soon after. The three sows of this generation were also impotent, so that in two consecutive brother and sister matings this family was entirely exterminated.

This is a single case and is not necessarily a typical result of inbreeding swine. It should be remembered that

several of Wright's inbred families of guinea pigs became extinct, while others were fully able to survive and were actually improved in certain characters. But such a disastrous result as this may occur with any farm animals. The Delaware Station also found that matings of related Berkshire pigs, where the degree of consanguinity was not closer than half brother and sister, gave unfavorable results. Altogether they observed 108 inbred litters and summarize their results as follows: "The certainty of pregnancy is reduced by inbreeding and smaller litters result. The birth weight is generally slightly greater for inbred pigs than for outbred or crossbred pigs due probably to the smaller number in the litter, but the mortality rate is higher and the rate of growth after birth and final weight is without exception less for the inbred offspring." Certain decided abnormalities were exhibited by some of the inbreds. On the other hand, many swine breeders have practiced close mating without apparently harmful results; although it is doubtful if any of them practice inbreeding as close as brother and sister mating, and if they do they seldom continue it for many generations in succession.

Results with poultry.—Dunn, of the Connecticut Storrs Station, finds that when chickens are closely inbred much the same results ensue as with swine. There is a notable falling off in size, general hardiness, and the number of eggs laid and the proportion of the eggs which hatch. Marked differences in these respects, however, are seen in the progenies of different individuals.

General results of inbreeding.—We thus see that inbreeding of the most intensive kind with animals does not necessarily always lead to degeneration and extermination. If carried out with large enough numbers and accompanied by rigid selection, it may even be beneficial in eliminating sterility, weaknesses, and abnormalities, bringing about uniformity, and intensifying particular qualities. These experiments with animals show no results that can not be interpreted as the result of the recombination of Mendelian

factors. What we want to know, however, is whether the results of inbreeding depend wholly upon the inheritance received, or partly upon the long-held assumption of harmfulness in consanguinity itself aside from the operation of heredity. Before we can decide this question satisfactorily, we must turn to hermaphroditic plants. Bisexuality, with the greater variability which this brings about, makes animals less suitable material with which to solve this problem.

Self-fertilized species.—Many wild species and numerous varieties of cultivated plants are almost always self-fertilized in every generation, and apparently lack nothing in vigor, productiveness or ability to survice. Among wild plants, many species of the family Leguminosae, and among cultivated plants, wheat, rice, barley, oats, tobacco, peas, beans, and tomatoes are characterized by very nearly continuous self-fertilization, and these plants are in no immediate danger of extinction.

Natural provisions for cross-fertilization.—On the other hand, many of the higher plants are provided with devices which promote natural cross-pollination, and show definite injurious effects when artificially inbred. Even species which are characteristically self-fertilized are crossed occasionally. This, together with the fact that nearly all plants and animals are benefited by crossing, led Knight, as early as the close of the eighteenth century, to believe that self-fertilization is not a natural process and always produces more or less injurious results. His views were summed up in the statement, "nature intended that a sexual intercourse should take place between neighboring plants of the same species." Darwin, fifty years later, basing his conclusion upon observations of animals and direct experimentation with plants, went even farther, and said that "nature abhors perpetual self-fertilization." In the light of our present knowledge, this epitome should be changed to the statement that "nature has found a great advantage in an occasional cross-fertilization."

Darwin's inbreeding experiments with plants.—Darwin compared self-fertilized plants with intercrossed plants in many different species. In the majority of cases, the self-fertilized plants were clearly inferior to the crossed plants. These facts led to the belief that the evil effects of inbreeding kept on accumulating until eventually a plant or animal continuously reproducing in that manner was doomed to extinction. His own experiments, however, did not indicate that this assumption was justified. The two plants with which inbreeding was practiced the longest, *Ipomea* and *Mimulus*, showed very little further loss of vigor after the first generation. The experiments did bring out most clearly, however, that there was segregation of the inbred stock into types differing in their ability to grow, as well as in minor, visible, hereditary characters. In both species, plants appeared which were superior to other plants derived from the same source, some being equal or even superior in vigor to the original cross-pollinated stock. The inbred plants differed from the original material most noticeably in the uniformity of visible characters. Darwin's gardener stated that it was not necessary to label the plants, as the different lines were so distinct from each other and so uniform among themselves they could be easily recognized.

After several generations of inbreeding, Darwin found that it made no difference in the resulting vigor whether the plants in an inbred lot were selfed or were crossed among themselves. This he correctly ascribed to the fact that the plants were alike in germinal constitution. He thought this similarity was largely due to their having been grown for several generations under the same conditions, but it is easy to see why he held so tenaciously to this view if one remembers the faith he had in the effect of environment on organisms. This view he considered to be supported by the fact that crosses between his inbred families did not give as large increases as when the inbred plants were crossed with different stock from another locality. His

crosses between inbred lines did give noticeable increases in growth, in many cases equaling the original variety.

With Darwin, we still attribute the greater increase of vigor in crosses of distinct stocks to a greater germinal diversity; but we differ with him as to the way in which the germinal differences were brought about. However that may be, great credit is due Darwin for being the first to see that increased growth is brought about not by the mere act of crossing, but by the bringing together of unlike germinal complexes. This he states clearly in the following sentences:

"A cross between plants that have been self-fertilized during several successive generations and kept all the time under nearly uniform conditions, does not benefit the offspring in the least or only in a very slight degree. *Mimulus* and descendants of *Ipomea*, named *Hero*, offer instances of this rule. Again, plants self-fertilized during several generations profit only to a small extent by a cross with intercrossed plants of the same stock (as in the case of *Dianthus*), in comparison with the effects of a cross by a fresh stock. Plants of the same stock intercrossed during several generations (as with *Petunia*) were inferior in a marked manner in fertility to those derived from the corresponding self-fertilized plants crossed by a fresh stock. Lastly, certain plants which are regularly intercrossed by insects in a state of nature, and which were artificially crossed in each succeeding generation in the course of my experiments, so that they can never or most rarely have suffered any evil from self-fertilization (as with *Eschscholtzia* and *Ipomea*), nevertheless profited greatly by a cross with a fresh stock. These several cases taken together show us in the clearest manner that it is not the mere crossing of any two individuals which is beneficial to the offspring. The benefit thus derived depends on the plants which are united differing in some manner, and there can hardly be a doubt that it is in the constitution or nature of the sexual elements. Anyhow, it is certain that the differences are not of an external nature, for two plants which resemble each other as closely as the individuals of the same species ever do, profit in the plainest manner when intercrossed, if their progenitors have been exposed during several generations to different conditions."

Key to the problem of inbreeding.—In Darwin's time, unfortunately, the key to the solution of the problem of

inbreeding was lacking. Mendel's work, although it was being done at this time, was not yet known, and the principles of inheritance of separate characters, of segregation and chance recombination, were still unfamiliar to many who could have made good use of them. Had Darwin realized that it is a common occurrence for recessive characters to be concealed for many generations without making their appearance until segregated out by inbreeding, surely his views on this subject would have been materially changed.

Experiments of East and of Shull with maize.—The greatest advance in knowledge of the significance of inbreeding has come through linking its effects with Mendelian phenomena. The first experiments on inbreeding made after Mendel's principles were known were those of East and Shull, begun independently in 1905 with Indian corn, an extensively cross-fertilized species, as the material used.

Shull observed that the progeny of every self-fertilized maize plant is inferior in size, vigor, and productiveness when compared with normal cross-bred plants obtained from the same source. He thus corroborated preceding investigations made by Morrow and Gardiner and by Shamel. He also found that the decrease in size and vigor did not proceed at a uniform rate or at an increasing rate, as might be inferred from previous opinions, but that the reduction soon became less pronounced and indicated an approach to stability. Shull fitted these observations with a Mendelian interpretation and pointed out that a field of corn could be considered as a collection of complex hybrids which could be sorted out into its elementary components automatically by self-fertilization.

The hybrid nature of ordinary corn plants and their dependence upon hybridity for their normal vigor was clearly shown by the decided differences obtained in definite, hereditary, characters shown by the descendants from different plants belonging to the same variety. If inbreeding is purely a process of sorting out into a homozygous condition different hereditary strains from a mixed lot, there are

several ways of testing this hypothesis. Obviously, the inbred strains, when once reduced to uniformity and constancy, should show no increase in size or vigor when different individuals belonging to the same homozygous strain are crossed together. Since each plant is like every other plant in its genetic constitution, when once completely reduced, it should then make no difference whether the plant is self-fertilized or crossed with other plants having the same construction. Crosses between different inbred strains should, in many cases, result in a marked increase in growth, but these hybrid plants should be no more variable than their uniform parents, since all the plants of the first generation result from the same combination of gametes. The second generation should be more variable and should again be reduced in yield. Furthermore, it should make no difference, if the inbred parents were completely homozygous, whether the hybrid plants were self-fertilized or crossed with each other. All of these tests Shull carried out after his strains had been inbred for five generations. The variability of two of these strains and the first and second year crosses between them, as shown by an easily measured character—number of rows of grain on the ear, is given as follows:

Strain	Mean	Coefficient of Variation
A	8.30±.06	8.50±.47
B	14.10±.15	9.66±.74
(A×B)F_1	12.71±.15	10.00±.87
(B×A)F_1	11.77±.07	8.13±.42
(A×B)F_2	11.84±.11	14.64±.67
(B×A)F_2	13.79±.11	10.62±.56

The inbred parental strains and the F_1 hybrids are equally uniform, while the second-generation reciprocal crosses are more variable. In making the other tests, nine different self-fertilized families of the fifth generation were

compared with families obtained by crossing two plants within each family; seven first-generation hybrids were made between different selfed strains; ten crosses between individual F_1 plants were compared with the progenies of self-fertilized plants within the same group; and ten lots of plants were grown which had been normally cross-fertilized for five years, thus representing the original variety. The average height in decimeters, number of rows of grain on the ear, and yield in bushels per acre of these fifty-five families follow:

	Selfed	Sib Crosses	F_1	$\frac{F_2}{F_1 \text{ Selfed}}$	$\frac{F_2}{F_1 \text{ Sib Crosses}}$	Cross-bred Variety
Average height....	19.28	20.00	25.00	23.55	23.30	22.95
Average no. rows..	12.28	13.26	14.41	13.62	13.73	15.13
Average yield.....	29.04	30.17	68.07	41.77	47.46	61.52

The sib crosses (sister × brother) show a slightly greater height, number of rows of grain on the ear, and yield per acre than the corresponding self-fertilized families, indicating as Shull states, that the inbred strains had not yet been reduced to complete homozygosity; in other particulars, Mendelian expectation was wholly confirmed.

The Connecticut experiments with maize.—These experiments of Shull on the result of inbreeding corn were carried on from 1905 to 1911. The experiments begun at the same time at the Connecticut Station have been continued beyond the fifteenth generation of continuous self-fertilization. The general method has been simply to self-pollinate individual plants from different varieties of all the principal types of maize. The progenies from such self-fertilized plants were grown and plants again self-fertilized. Thus a single selfed plant has been the progenitor of each inbred generation. Dent, pop, flint, sweet, and floury types have been used, and many varieties of each have been inbred for

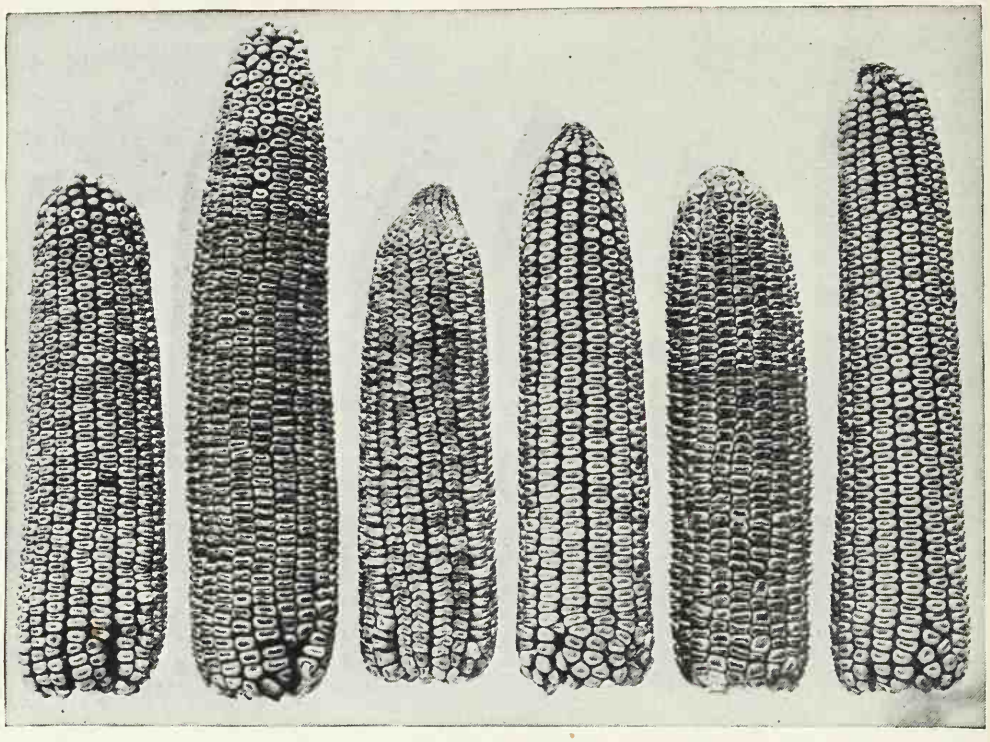


FIG. 131.—Representative ears of Leaming corn with which inbreeding experiments were begun. The specimens shown are the largest ears from sixty plants.

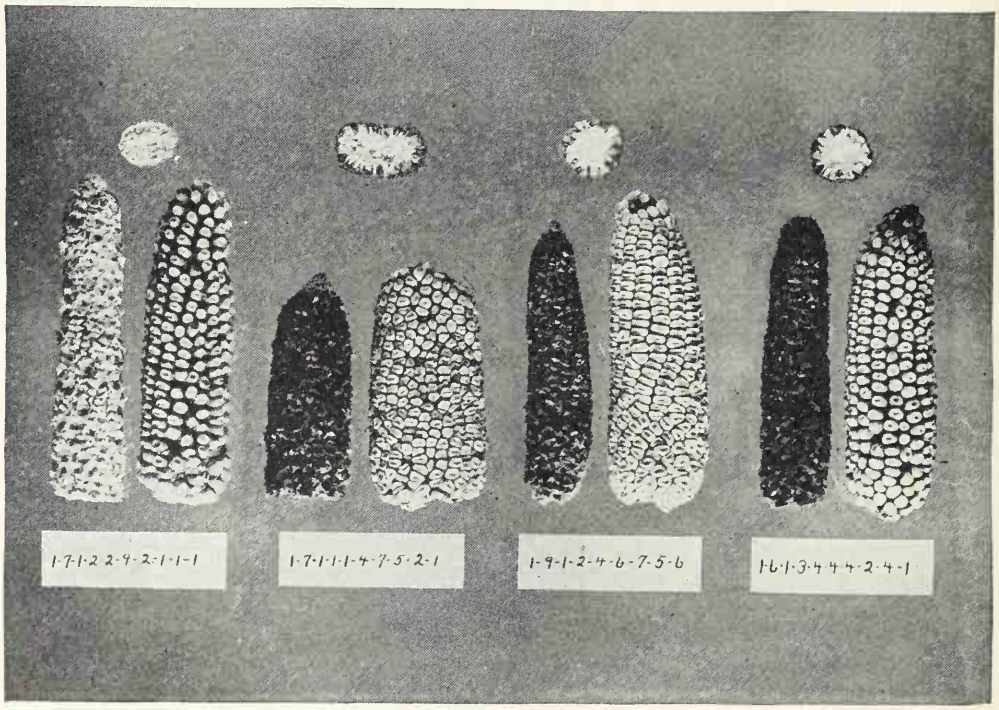


FIG. 132.—An ear, a cob, and a cross-section of a cob of four inbred strains of Leaming corn after nine generations of self-fertilization.

at least several years. Principal attention has been paid to four inbred strains descending from four plants originally out of Leaming corn grown in Illinois. These have been the longest inbred. Three other strains from Illinois high and low protein selections, originally out of Burr's White Dent, also from Illinois, have been inbred for many years, and also four strains from a local variety of Leaming corn grown in Connecticut for many years. The observations also include over a hundred inbred strains which have been inbred for several generations.

Segregation of characters.—In every case there has been a reduction in size and yield of grain. The several inbred lines originating from the same variety have become more or less strikingly differentiated in morphological characters. Some of the differences which characterize the several inbred strains in various combinations are as follows:

Colored and colorless pericarps, cobs, silks, and glumes.
Profusely branched tassels and scantily branched or unbranched tassels.
Long ears and short ears.
Round cobs and flattened cobs.
Narrow silks and broad silks.
Ears with various numbers of rows of grain.
Ears with straight rows and ears with irregular rows.
Ears with large seeds and ears with small seeds.
Ears with dark-yellow seeds and ears with light-yellow or colorless seeds.
Ears high on the stalk and ears low on the stalk.
Stalks with many tillers and stalks with few tillers.
Leaves with straight margin and leaves with wavy margin.
Leaves broad and narrow.

Appearance of unfavorable characters.—Many other character differences governed by definitely inherited fac-

tors have been observed, but these may serve as illustrations. They are common variations seen in almost every field of corn. They are all normal characters in that they do not hinder the plant in its growth and reproduction. Many other characters appear which are clearly abnormal. They prevent the plants from growing as they should, and handicap them in the cultivated field as well as in nature. White seedlings which lack chlorophyll are seen in small numbers in nearly every field of corn. Various

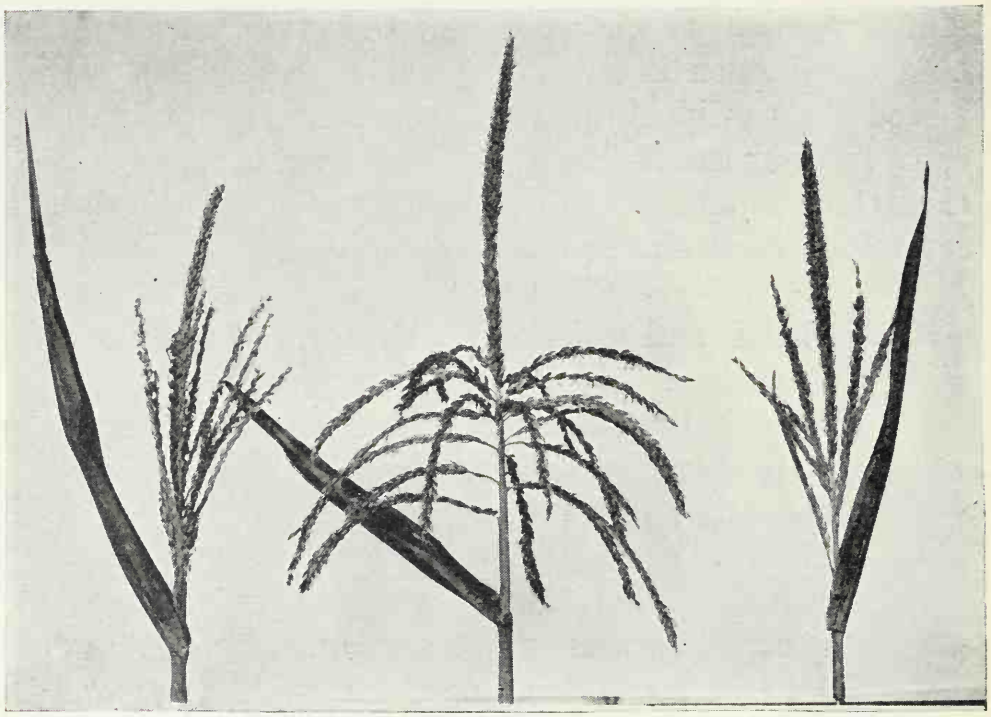


FIG. 133.—Characteristic tassels from three inbred Leaming strains of corn.

other degrees of deficiency in green coloring matter are not unusual in corn and are among the commonest variations in inbred families. A number of different kinds of striping are obtained, as well as plants which are yellowish green, light green, and dark green. Many of these types have difficulty in struggling through to seed production and are hard to maintain as a pure strain. The white and yellow seedlings are unable to live beyond the stage made possible by the food stored in the seed. Another common abnormal

type is that of the dwarf plant. Corn plants of low stature are frequently obtained in inbred cultures, and also occur in ordinary corn fields. These plants differ markedly in growth and reproductive ability. Some make pollen and set seed freely. Others are very difficult to keep alive in a pure state. Many types of ear malformations are found, and a number of conditions of sterility affecting the pollen, tassels, and ears. Some plants lack brace roots and are unable to stand upright. Many clear manifestations of differences in susceptibility to parasitism by smut, rust, and blight organisms are brought out, as well as differences in the

FIG. 134.—Seedlings entirely lacking in chlorophyll and unable to live beyond the stage made possible by food stored in the seed.

reduction of chlorophyll in the leaves during the latter part of the growing season. The variability of the inbred strains in respect to all these characters decreased as inbreeding was continued. After four generations they were practically constant for the grosser characters. From the eighth generation on, they have been remarkably uniform in all characters.

General results of inbreeding maize.—The results of inbreeding the naturally cross-fertilized maize plant can be briefly summarized as follows:

1. There is a reduction in size of plant and in productiveness, which continues only to a certain point.

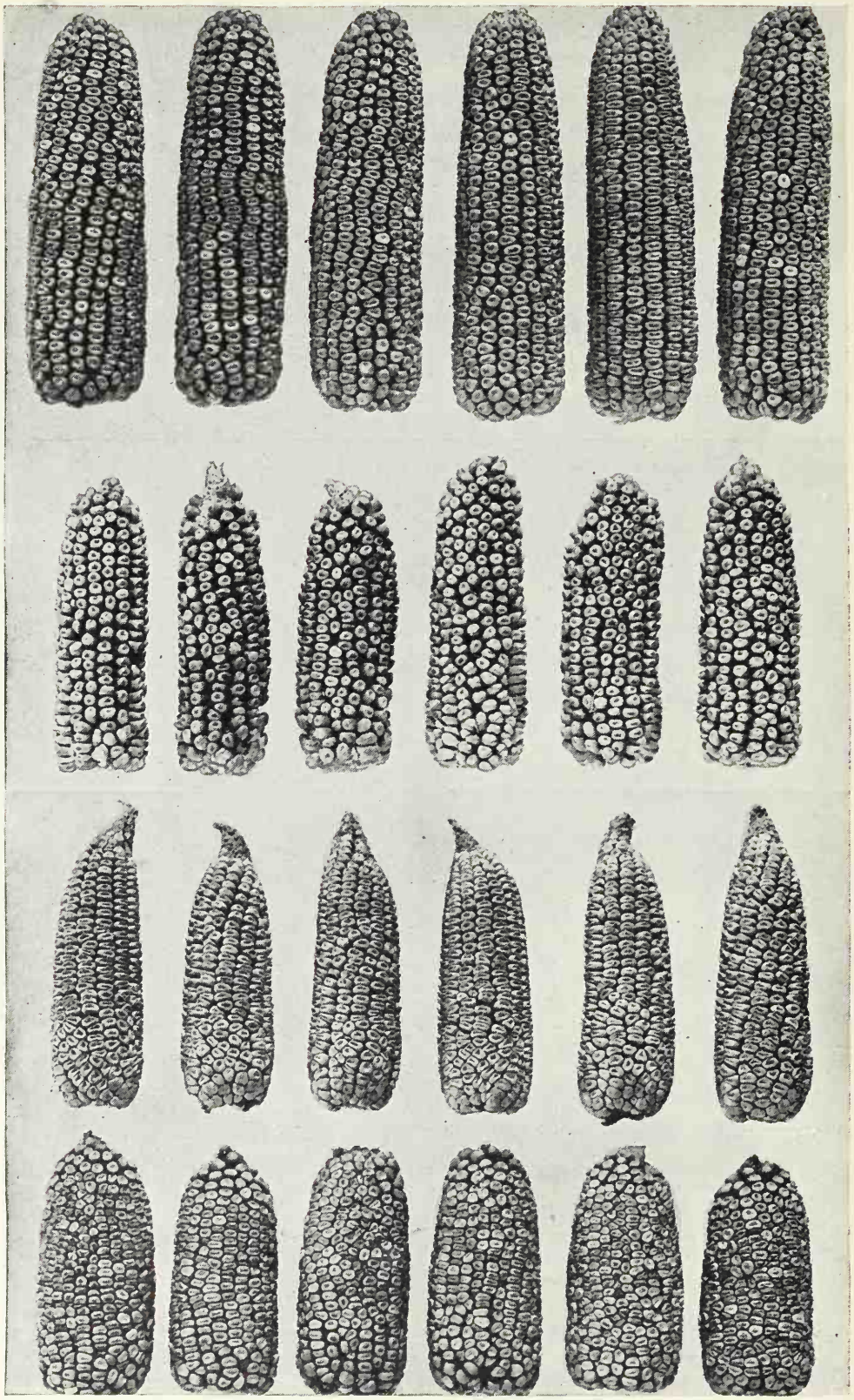


FIG. 135.—Four inbred strains of Leaming corn, derived from the variety shown in Fig. 131 and reproduced on the same scale.

2. There is an isolation of subvarieties differing in morphological characters accompanying the reduction in growth.

3. As these subvarieties become more constant in their characters, the reduction in growth ceases to be noticeable.

4. Individuals are segregated out with such characters that they can not be reproduced or, if so, only with extreme difficulty.

5. Strains differing in amount of growth and productiveness are finally obtained, and these remain at their respective levels of vigor from year to year, with no appreciable change. So far, they have all been less vigorous and lower-yielding than the original variety.

This summary is based upon all the material worked with. A large amount of data has been accumulated. A few illustrations will show the general result. The strains which have been the longest inbred will serve to show something as to the effect inbreeding has had upon the yield of grain, height of plant, and other characters.

The inbred Leaming strains.—The original Illinois Leaming variety was given the number 1. A number of plants were self-fertilized in 1905. Four of these were grown and were numbered 1–6, 1–7, 1–9, and 1–12. These four lines were perpetuated each year by self-fertilization. In the second inbred generation two self-pollinated plants in line 1–7 were saved for seed, and two lines were grown from them from that time on. These are 1–7–1–1 and 1–7–1–2. They both trace back to the one strain inbred for two years. The many other inbred strains which have been carried along with these need not be mentioned specifically, except as they bring out special features.

Decrease in yield.—The yield of grain and height of plant are given in Table XXIX for the successive generations of self-fertilization. The original variety in Illinois in 1905 yielded at the rate of 88 bushels per acre. In 1916, seed of the same variety obtained from the same original source was grown in Connecticut and yielded at the rate of 75 bushels of shelled grain. There is no reason for supposing

TABLE XXIX

THE EFFECT OF SELF-FERTILIZATION UPON THE YIELD AND HEIGHT OF CORN

Number of Generations Selfed	Four Inbred Strains from Leaming Dent Corn							
	1–6–1–3, Etc.		1–7–1–1, Etc.		1–7–1–2, Etc.		1–9–1–2, Etc.	
	Yield, Bushel per Acre	Height, Inches	Yield, Bushel per Acre	Height, Inches	Yield, Bushel per Acre	Height, Inches	Yield, Bushel per Acre	Height, Inches
0	75	117	75	117	75	117	75	117
1	59	...	61	...	61	...	42	...
2	95	...	59	...	59	...	52	...
3	58	...	46	...	60	...	35	...
4	80	...	63	...	68	...	48	...
5	28	87	25	81	41	91	26	77
6	...	...	...	...	...	...	40	..
7	42	...	39	...	...	...	45	85
8	79	96	47	84	59	88	22	...
9	26	...	25	...	...	...	31	79
10	33	98	33	85	19	87	32	82
11	46	104	42	79	38	84	35	80
12	50	100	27	80	20	85	25	77
13	26	85	29	84	25	81	27	86
14	35	94	38	87	36	88	24	87
15	34	100	33	90	30	98	...	...
0	75	117	75	117	75	117	75	117
1–5	64	87	51	81	58	91	41	77
6–10	45	97	38	85	39	88	34	82
11–15	38	97	34	84	30	87	28	82

that the variety had changed materially in the intervening years, although there is no way of comparing the variety from Illinois with the inbred strains which have been grown in Connecticut and naturally selected for these conditions for many years. But even with this in favor of the inbred strains, they yielded only from one-third to one-half as much as the crossbred variety under the same conditions.

As to the rate of reduction in yield or the constancy of the inbred lines during the later generations, it is difficult to draw any conclusions from these figures, owing to the seasonal changes from year to year and to the difficulty of accurately testing yield with a small number of plants under field conditions. No figures as to yields are available for the year 1912. The yields for 1909, 1911, and 1915 were low on account of poor seasons. In 1914 they were high for the opposite reason. In some of the years, the number of plants grown was small and the results are correspondingly unreliable. In 1916 and 1917 the inbred strains were grown in good-sized plots and the yields for those years are fairly reliable.

Examining the table with these points in mind, we find that there has been a marked falling off in productiveness, from the yield of the variety at the start, up to the ninth generation. In that generation the plants were on the average only one-third as productive as the variety before inbreeding. From the ninth generation on, there has been no consistent reduction in yield and practically no change in visible features. Height of plant, as far as the figures are available, followed the same general course. The reduction has practically all taken place in the first eight generations of inbreeding; after that there has been no appreciable change.

The several strains have differed from the start in productiveness and height, and this is correlated with the size of stalk and general vigor of the plant as expressed in its rate of growth and healthy green color of foliage. Strain 1–6 has, with few exceptions, been the highest in yield and produced the tallest plants. Its yield was nearly 50 percent greater in the eleventh generation than that of the poorest strain, and it was nearly 30 percent taller than that of the shortest strain.

Lines which can not be perpetuated when inbred.—Strain No. 1–12 grew so poorly in the sixth generation that no seed was obtained that year, and as all the seed of

previous generations had been planted or failed to germinate this strain was lost. All along, it had been the poorest of the five. The ears were small and poorly filled out at the tip, and it was carried along only by considerable effort. There is difficulty in perpetuating any self-fertilized strain, owing to the failure to pollinate at the correct time, unfavorable weather at pollinating season, loss of ears enclosed in paper bags, due to mold, and the low viability of the seed. The loss of this strain might have been the result of a combination of bad circumstances without assuming continuous deterioration. The strain probably could have been retained if sufficient effort had been put forth; but in view of the further reduction in other strains, it would have been extremely difficult. Plants which can not be perpetuated, on account of the unfavorable characters they possess, are frequently produced; and it is quite possible, therefore, that some strains will be found that are unable to survive no matter how many individuals are produced. This is evidence that strains differing markedly in their ability to grow are isolated by inbreeding.

Effect of inbreeding on pollen production.—Many inbred strains of corn show an extreme reduction in the amount of pollen produced. These strains are often among the best in ear formation, but in order to produce the yields which they give in open field culture, they are dependent upon other strains growing near by for an adequate supply of pollen. Other strains lack nothing in pollen production, and some in fact are more prolific in this respect than many variety plants. Such strains are usually below the average in number and size of seed produced. Inbred plants which are good in both pollen and ovule formation are obtained but rarely. This would be expected on the basis of chance alone, if the two sex functions were independent of each other, since it is more difficult to secure two things together than it is to obtain either alone. However, there is some indication that when the plants are unable to maintain both functions normally they favor one or the other.

Attainment of complete homozygosity.—The plants of those strains which survive, while smaller in size and lower in yield of grain, are perfectly healthy and normal in every way. All factors for total sterility have been eliminated, and abnormal and seriously unfavorable characters no longer appear. The figures given in Table XXIX show that these inbred strains have reached the limit of their reduction in size and productiveness, and that whatever changes have taken place in the last six years have been unimportant. Whether or not complete homozygosity, with its concomitant uniformity and constancy, has been reached, can not be told positively until these strains are carefully tested; but crosses within these strains, made in the ninth generation, showed no significant increases when compared with selfed plants in the same line. It seems apparent, therefore, that the falling off in vegetative vigor and productiveness is very nearly, if not quite, at an end.

Similarity of effects of inbreeding and of poor environment.—Along with the reduction in yield, height, and size of ear, there is also a decrease in such characters as number of nodes on the stalk and rows of grain on the ear, but in contrast with the other three characters the change is slight. The last two are only slightly affected by environmental characters, as compared with the others. By being grown on poor soil, a corn plant may be reduced to half its normal height, but the number of nodes will be nearly the same in the two cases. Hence, we see that inbreeding affects plants in much the same way as poor environmental conditions.

Reduction in variability accompanying segregation of type.—There is a reduction in variability and change in mean in all the characters of the plant. This is shown in Table XXX in which the number of rows of grain on the ear are given for the original Leaming variety and the four strains derived from this after ten generations of self-fertilization. The restricted range of the inbred lines and their coefficients of variability bring out clearly the great

TABLE XXX

FREQUENCY DISTRIBUTION OF THE NUMBER OF ROWS OF GRAIN ON THE EAR OF THE ORIGINAL VARIETY OF CORN AND FOUR INBRED STRAINS DERIVED FROM IT

Pedigree Number	Number of Rows of Grain on the Ear								Total	Average	C. V.
	12	14	16	18	20	22	24	26			
Variety	3	14	51	75	52	21	7	4	227	18.4±.12	14.2±.46
1–6–1–3, Etc.	11	90	86	26	6	..	..	..	219	15.3±.08	11.1±.36
1–7–1–1, Etc.	..	..	1	22	56	78	43	6	206	21.5±.09	9.4±.31
1–7–1–2, Etc.	..	24	42	18	1	..	..	..	85	15.9±.11	9.2±.48
1–9–1–2, Etc.	..	39	70	3	2	..	..	..	114	15.4±.08	7.8±.35

reduction in variability. This reduction is only for each inbred line considered by itself. If all the possible lines were grown and all were combined together into one population, the variation would be greater than that shown by the cross-fertilized variety. This is indicated by the figures available; it also follows from the fact that many characters which are seldom seen in the regularly cross-pollinated stock are brought to light by inbreeding. We should, therefore, see clearly that crossing reduces the visible variation in the population as a whole, but that the potential variability is increased. This is brought out by inbreeding. The diversity of the descendants taken all together is increased, but the variability within each inbred line is markedly decreased.

From a theoretical standpoint, as will be shown later, the production of nearly homozygous individuals by self-fertilization is greatest in the generations from the third to the sixth, if a large number of factor differences are involved at the start. The results from the inbred plants so far obtained seem to fit this theory. While there is a reduction in size and productiveness from the start, it is not until the third generation that extremely abnormal types begin to appear. While they may theoretically appear from the start, and many of them do, it is usually not until

after three successive self-fertilizations that the greatest diversity of types occurs. There will be great differences between different lines in this respect. Some will be quite uniform and stable by that time, while others will show great variation. It is in the generations from the third to the sixth that most of the monstrosities and plants which are unable to reproduce themselves appear.

Change in row number.—Equally striking changes in mean row number take place at this time, as shown in

TABLE XXXI

REDUCTION IN VARIABILITY AND CHANGE IN EAR ROW NUMBER IN INBRED STRAINS OF CORN

Generations Selfed	Inbred Strain	Number of Rows of Grain on the Ear									Total	Average	C. V.
		12	14	16	18	20	22	24	26	28			
3	A	3	3	4	6	27	7	4	1	2	57	19.7±.30	17.0±1.10
3	B	..	..	..	..	..	..	..	..	..	..	.....	.....
4	A	..	2	5	11	17	19	6	1	..	61	20.2±.22	12.7± .78
4	B	..	..	2	8	14	9	5	1	..	39	20.5±.25	11.2± .86
5	A	..	..	3	4	10	16	4	1	..	65	20.9±.25	10.9± .85
5	B	..	..	14	29	21	1	..	..	..	65	18.3±.13	8.3± .49
7	A	..	..	1	3	5	1	..	..	..	10	19.2±.34	8.3±1.26
7	B	..	4	12	2	..	..	..	..	..	18	15.8±.18	7.2± .80
8	A	..	..	..	1	9	16	6	..	..	32	21.7±.18	4.7± .40
8	B	..	..	17	20	6	..	..	..	..	43	17.5±.14	7.8± .57
9	A	..	..	..	1	14	4	2	..	..	21	20.7±.21	6.9± .72
9	B	..	6	16	7	..	..	..	..	..	29	16.1±.17	8.3± .74
10	A	..	..	1	10	13	11	1	..	..	36	20.1±.20	8.9± .71
10	B	..	12	22	8	1	..	..	..	..	43	15.9±.15	9.4± .68
11	A	..	..	3	20	43	22	7	..	..	95	20.2±.13	9.2± .45
11	B	3	23	45	22	2	..	..	..	..	95	15.9±.11	10.4± .51

Table XXXI. The averages have been shifted up and down from the original position. The greatest segregation has taken place before the eighth generation. In that year the lines were again split up, but show no marked changes since then.

The figures showing the rate of reduction in variability and speed of the change in average row number, given in Table XXXI, are plotted graphically in Fig. 136. These two lines are descended from one plant in the second year

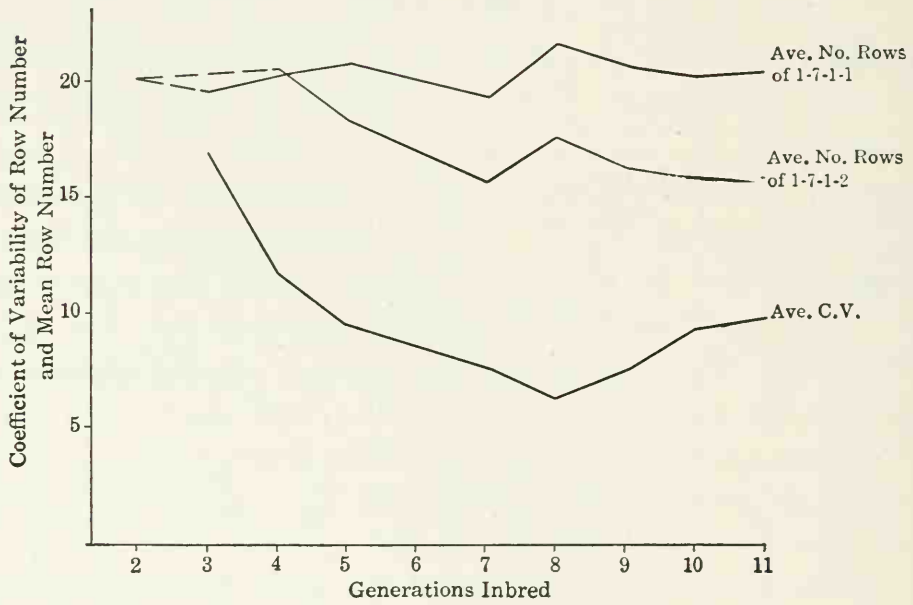


FIG. 136.—Change in average row number and reduction in variability plotted on the same scale.

of self-fertilization. The figures previous to the third year are not available, and in that year for only one of the two strains, but after the third generation there has been a marked change in mean row number, and a reduction in variability without selection one way or the other.

The number of plants grown in the generations from the seventh to the tenth are too few to be a basis for critical comparison. The sharp increase in row number and decline in variability in the eighth generation is most probably due to the favorable growing conditions, as seen in the

table of yields given previously. The apparent rise in variability after the eighth generation is in part due to the

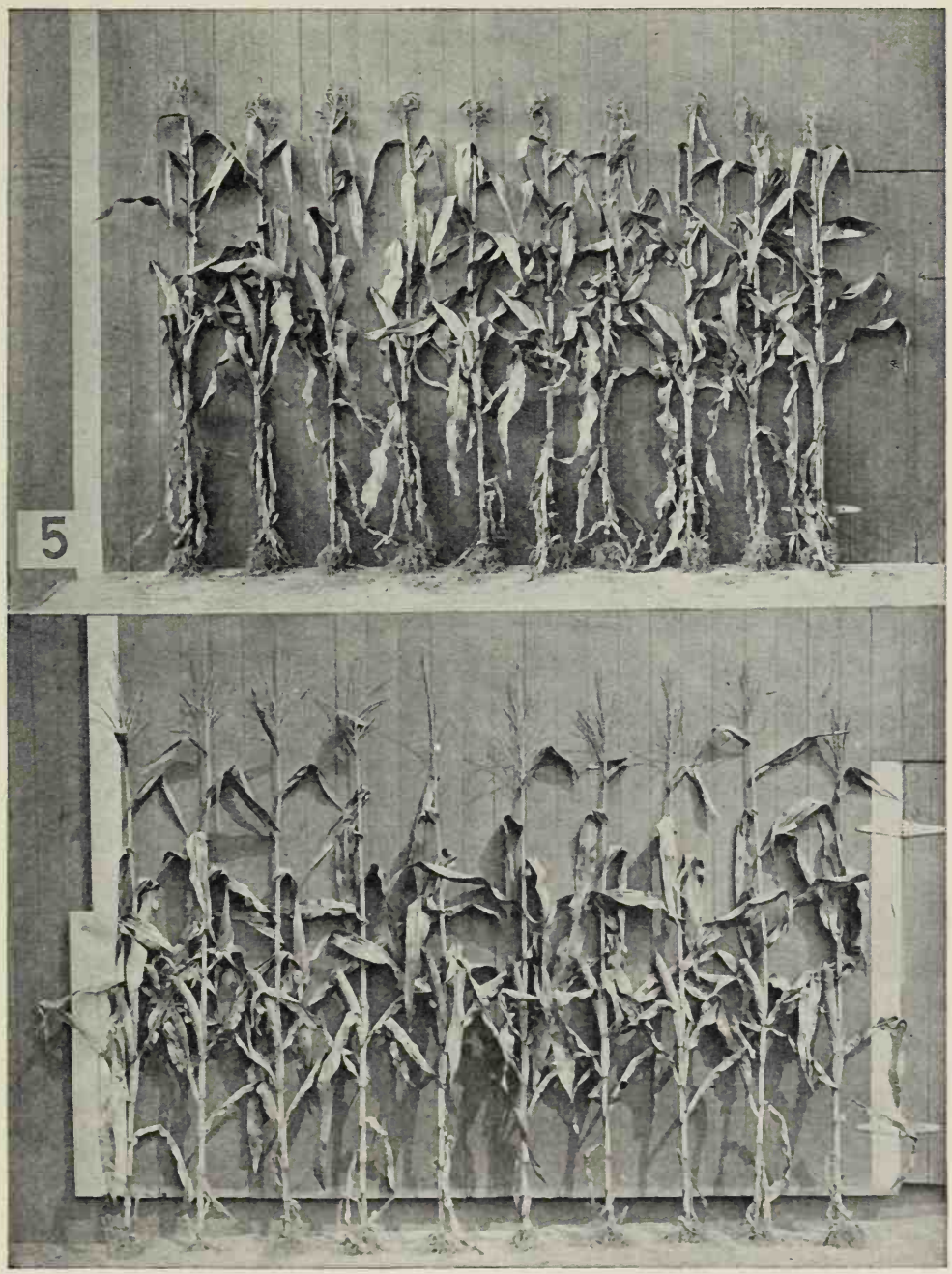


FIG. 137.—Two inbred strains of Leaming, showing uniformity in structural details within the strains and differences between them.

fact that the ears have become somewhat more irregular in row number, and the determination of the actual row number

has therefore been somewhat more difficult in the later generations.

Uniformity in structural details.—The details of the plant and ear structure, statistical treatment of which is difficult, show the effect of inbreeding upon variability most clearly. The beautiful uniformity of these plants in all characteristics is their most outstanding feature at the present time. This can be seen fairly well for the ear characters in the accompanying illustrations. In the form, arrangement, shade of coloring and various peculiarities, the tassels, leaves, and stalks show the same striking uniformity. These minor details which distinguish each of these groups of plants can not be described adequately, but are the most noticeable feature about them. The tassels or the ears of these four Illinois Leaming strains, if mixed together, could be separated without difficulty.

Susceptibility and resistance to disease.—In the same way, such indefinite and complex characters as susceptibility and resistance to disease are shown to be capable of segregation. One of the inbred Leaming strains has regularly shown less smut infection, and when the disease is present it is much less severe than with other strains in adjoining rows. The behavior of the four strains during five years in respect to parasitism by the smut fungus (*Ustilago Zeae*) is shown in Table XXXII. In 1917 and 1918, strain No. 1–6–1–3 had not more than 1 percent of the plants affected in nearly one thousand plants grown in each of the two years, whereas strain No. 1–7–1–1 had from 10 to 25 percent badly injured plants under the same conditions. Several plots of each strain have been grown in different parts of the field, and the different strains have been grown side by side, so that there is no way of accounting for the differences except in some feature inherent in the strains themselves. There is considerable variation from year to year, showing that much depends upon the weather conditions in relation to the time of growth of the plants, the amount of infection, and many conditions probably

TABLE XXXII

DIFFERENCES IN THE NUMBER OF PLANTS ATTACHED BY THE SMUT FUNGUS, *Ustilago Zeae*

Strain Number	1917		1918		1919		Total	
	Number of Plants	Percent Smut	Number of Plants	Percent Smut	Number of Plants	Percent Smut	Number of Plants	Percent Smut
Inbred strain 1–6–1–3.	992	0	1000	1.00	144	1.39	2136	0.56
Inbred strain 1–9–1–2.	596	.34	559	.71	157	1.91	1312	.69
Inbred strain 1–7–1–2.	408	.49	307	9.12	145	4.14	860	4.19
Inbred strain 1–7–1–1.	950	9.79	599	25.87	198	8.59	1747	15.17
(1–6–1–3×1–9–1–2) F_1	.....	.....	31	0	.....	.....	31	0
(1–6–1–3×1–7–1–2) F_1	.....	.....	435	0	3911	3.14	4346	2.83
(1–6–1–3×1–7–1–1) F_1	439	2.28	326	.61	.....	.....	765	1.57
Original variety.....	114	1.75	250	.40	119	7.56	483	2.48

yet unknown; but a degree of resistance to this organism is unquestionably inherited, and the factors which determine this are segregated into some lines and not into others by inbreeding.

Surviving inbred plants normal and healthy.—In spite of the fact that there has been a pronounced decrease in size, general vegetative vigor, and productiveness, and that in comparison with non-inbred varieties the inbred plants are more difficult to grow, emphasis must be put on the fact that they are normal and healthy. In one sense, no actual degeneration has taken place. The monstrosities which are frequent in nearly every field of maize, such as the occurrence of seeds in the tassels, anthers in the ears, dwarf plants, completely sterile plants, and other similar anomalies, now no longer appear in most of these inbred strains. These facts demonstrate beyond doubt that most of the variability found among ordinary cross-fertilized plants is due to the segregation and recombination of definite and

constant hereditary factors. Many characters which long-continued inbreeding brings to light are seldom seen in regularly cross-pollinated plants, and never are so many gathered together in one individual. This is due to the fact that they are recessive in nature and complex in mode of inheritance. Undoubtedly many of the characters which make their appearance in inbred plants may be modified by the vigor of the plants upon which they are borne, but it is significant that none of them can be attributed directly to a loss of a physiological stimulation. There is no one specific feature common to all inbred strains, but simply a general loss of vigor, a general reduction in size and productiveness, accompanied by specific characters more or less unfavorable to the plant's best development. But these unfavorable characters are never all found in one inbred strain, nor is any one of them found in all inbred strains.

Automatic elimination of weaknesses.—With the four Illinois Leaming strains upon which these observations are chiefly based, no conscious selection has been practiced. The plants to be hand-pollinated were taken at random and the ears for planting were chosen without particular regard to their size and form. Nevertheless, there has been a great deal of natural selection as is unavoidably the case with any inbreeding experiment. The difficulties of artificial pollination with maize result in the selection of plants whose tassels and silks appear at about the same time. Any difference in this respect, and especially a tendency towards earlier maturity of the pollen-bearing flowers, renders self-fertilization difficult or impossible, as corn pollen is viable but a short time. All plants that are weak, sterile, diseased, or in any way abnormal tend to become eliminated whenever these manifestations interfere with seed production. This unconscious selection becomes more rigid in the later generations as reduction in vigor and productiveness becomes more pronounced. Finally, the small amount of seed produced when pollination is con-

trolled, even under the most favorable conditions, necessitates the using of ears for planting which have a reasonable amount of seed in order to secure enough plants upon which to make any fair observations.

Tendency to delay homozygosity.—All these factors tend to prevent the attainment of complete uniformity and

FIG. 138.—A plant with narrow leaves, brought to light by inbreeding, that is unable to persist in competition with normal plants.

stability. In spite of this, all indications show that many inbred strains, particularly those which have been self-fertilized for fifteen years, are very nearly, if not completely, homozygous in all inherited characters. As brought out before, this evidence is comprised in cessation of reduction in size and productiveness, of reduction in variability,

and of change of average row number and other characters. Moreover, crossing between different members of one strain makes no appreciable difference in their offspring when compared to self-fertilized plants of the same line. In other words, all plants have the same composition of hereditary factors and it makes no difference how they are mated as long as no new factors are brought in. This is a complete demonstration of what Darwin insisted upon—

FIG. 139.—First-generation hybrid resulting from the cross of two of the inbred strains shown in Fig. 135.

that crossing itself was without effect and that the results depended upon the hereditary construction of the ensuing plants.

Uniformity of first generation crosses between homozygous strains.—When these uniform inbred strains, which are reduced in size and vigor, are crossed, there is an immediate return to the original large growth of the variety at the start, but with this noticeable difference: All the hybrid plants in the first generation are exactly alike. The uni-

formity is fully equal to that of their inbred parents. In height, type of tassel, and details throughout the plant's structure, there is a remarkable evenness, which is almost unbelievable to one who is familiar with the great diversity among individual plants in a common field of corn. But this uniformity lasts for only one generation, as we should expect. When these hybrid plants are again self-fertilized or bred among themselves (it makes no difference which,

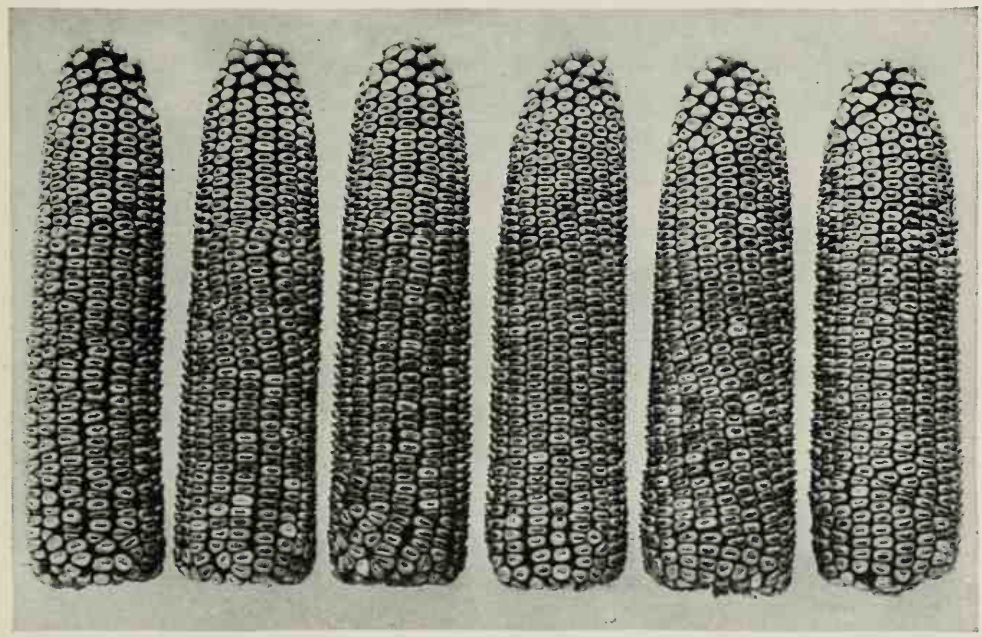


FIG. 140.—Ears produced by plants of the same type as shown in Fig. 139. These are the six largest specimens from sixty plants, grown in the row adjoining the plants which gave the ears shown in Fig. 131 and are reproduced on the same scale.

because all the plants in this first generation are alike in their germinal composition and are producing exactly the same segregating gametes), there is an immediate falling off in size, uniformity, and productiveness. If the plants were allowed to intercross naturally from then on, they would remain at about the same level of vigor and would continue to show the same variation. In growth and variability they would be quite similar to the original variety. When again self-fertilized from generation to generation, they

repeat the same process as when first inbred. Reduction in size and approach to uniformity proceed at the same rate as before, and the resulting inbred strains usually reach the same level of vigor in about an equal number of generations as when first inbred. This is shown in the accompanying illustrations. The final families which come from different plants in the second hybrid generation differ from

FIG. 141.—First-generation hybrid between two inbred strains, showing the evenness in height and uniformity in tassel type. The two parental strains are at the left of the tall hybrid plants.

each other as strikingly as the parental inbred strains differed, and they will be unlike their parents also, having a different combination of characters.

Nothing of value permanently lost by inbreeding.—It is thus clearly demonstrated that inbreeding works automatically to sort out different hereditary complexes. Hybrid vigor results from crossing unlike forms and is lost by inbreeding, but may be regained at any time by again

bringing together the same combination of elements which made for vigor in the first place, or an equally good one. It is a transitory unfixable result, for the most part, because of the difficulty, and in fact, practical impossibility, of recombining in one individual all the dominant favorable growth factors. The important consideration is that if weakness results from inbreeding there has been no permanent loss. All the elements which go to make up large size and strength are still there, scattered about among different individuals, but capable of being reassembled.

Similar results with alfalfa.—These results with corn have been duplicated with other plants. An extensive series of inbred strains of alfalfa, produced at the Arizona Station by Freeman after several generations of self-fertilization, showed clearly the approach to uniformity within, and differences between, the several inbred families. There was also a noticeable decline in size and vigor, particularly apparent in reduced seed formation.

Inbreeding cucurbits.—Sinnott, at the Connecticut Agricultural College, has obtained remarkably uniform families of squashes by inbreeding. Many forms of sterility, abnormalities, and weaknesses have shown up, but by selection several families have stood up much better, apparently, than any inbred strains of corn and in productiveness compare quite favorably with their parental crossbred stocks. Their fixity of type is a decided advantage in a garden plant which is extremely variable.

Cross-fertilized plants may be homozygous.—The long and vigorous selection which wild species have had to undergo under natural conditions makes it possible that cross-fertilized plants in the open may be in a state of near homozygosity, even though continually crossed. Many of them are as uniform and fixed in their type as self-fertilized species under the same conditions, and such forms would certainly not be expected to show such profound changes when artificially inbred as cultivated plants. Some wild cross-fertilized species, however, are reduced by inbreeding,

as Darwin found by comparing progenies from self-fertilized seed of plants growing naturally with those from the same plants which had been intercrossed with other members of the same species.

The tar-weed (*Crepis capillaris*) a member of the chicory tribe, is a native of Europe which has been unintentionally introduced into this country, where it grows as a common weed in certain localities. This wild plant, which is cross-fertilized under natural conditions, has been inbred by

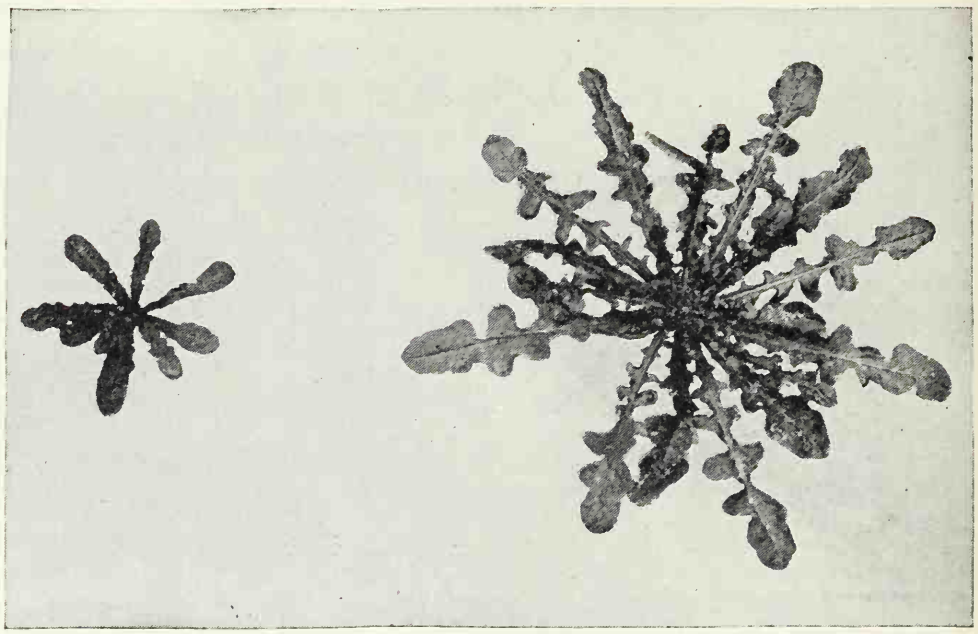


FIG. 142.—A self-fertilized plant (left) and a cross-fertilized plant (right) of the tar weed, *Crepis capillaris*. (After Collins in Jour. Heredity.)

J. L. Collins, and the unfavorable results obtained compare very closely with those from maize (Fig. 142). This is not the usual result to be expected from uncultivated species, and some crossing with other forms may have taken place before it was inbred. The fact is clear, nevertheless, that the reducing effects of inbreeding are not limited to cultivated plants.

Segregation mathematically illustrated.—The automatic sorting out of a heterozygous factor complex into a number

of different homozygous pure-breeding individuals, and from them families, can be illustrated in its simplest form in the following way. A plant or animal which is heterozygous in one factor pair, Aa, will produce three kinds of offspring when self-fertilized or bred to another individual having the same composition. These will be 1AA, 2Aa and 1aa, the simple Mendelian formula. In this progeny 50 percent are homozygous and will remain so as long as they are not paired with individuals of different composition. The other 50 percent are heterozygous, like their parent, and will again split in the same way. In the next generation, therefore, if all classes reproduce and are equally fertile, there will be 75 percent pure-breeding individuals and 25 percent which again split up. The curve in reduction of hybrid individuals proceeds by halving the remaining difference in each generation, because the homozygous individuals when once formed remain homozygous and the heterozygous individuals are reduced 50 percent in each generation. This gives a series of percentages of heterozygous individuals resulting from each successive self-fertilization, as follows: 100, 50, 25, 12.5, 6.25, 3.125, 1.5625, .78125, etc. After seven continuous self-fertilizations, the number of heterozygous individuals which will not breed true is reduced to less than 1 percent. The others are of two types, AA and aa, and will remain unchanged until outcrossed.

This procedure will be followed irrespective of the number of heterozygous factor pairs concerned at the start. Each pair will be reduced by 50 percent in every generation independently of all the others, and so the theoretical curve of inbreeding for the population as a whole is the same, no matter how complex the degree of hybridization at the commencement of inbreeding. But the probable number of completely homozygous individuals in each generation depends upon the number of factor differences at the start. The proportion of complete homozygotes to the different classes of heterozygotes in any generation r

is found by expanding the binomial $1+(2^r-1)^n$ where n represents the number of factor pairs involved. The exponent of the first term gives the number of heterozygous and the exponent of the second term the number of homozy-

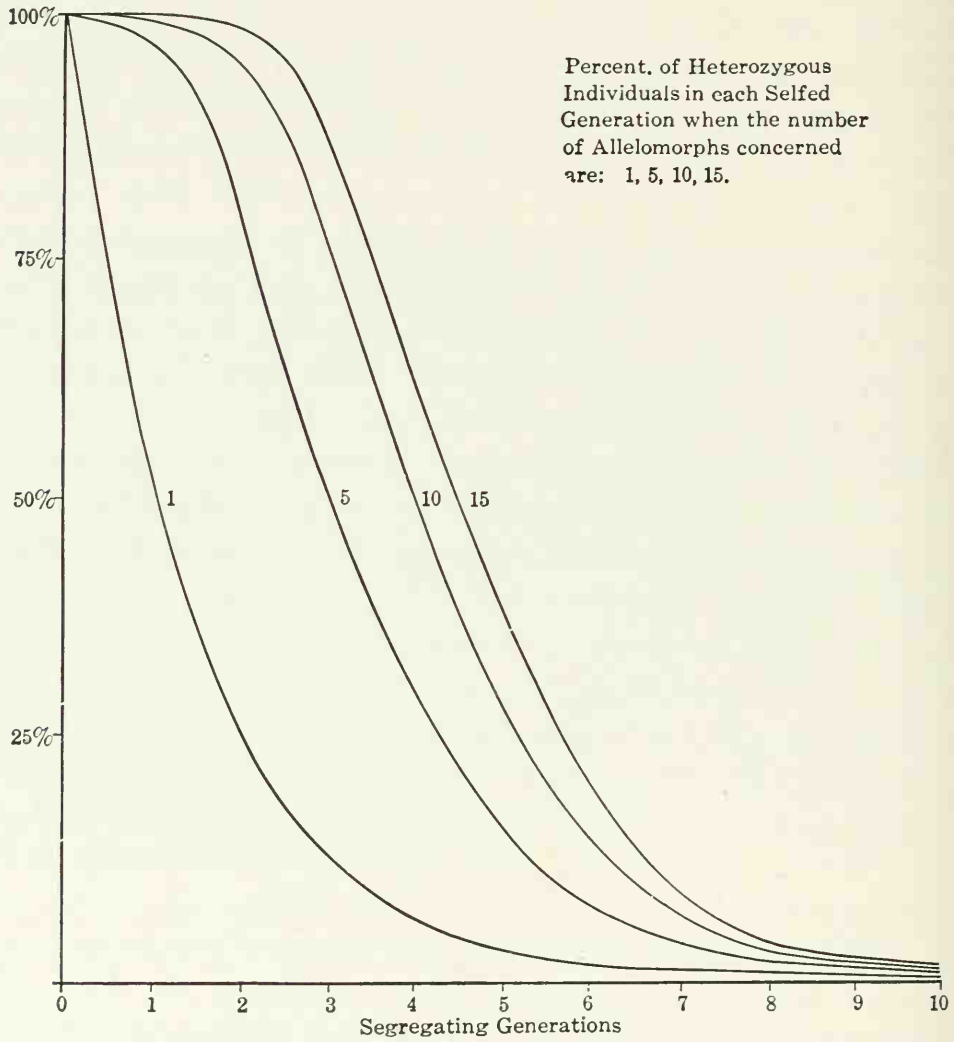


FIG. 143.—Diagram showing the percent of heterozygous individuals and of heterozygous allelomorphic pairs in the whole population in each generation of self-fertilization.

gous factors. As an example, suppose we desire to know the probable character of the fifth segregating generation (F_6) when self-fertilized, if three factor differences are concerned at the commencement of inbreeding. Expanding, we get $1^3+3(1^2(31))+3(1(31)^2)+(31)^3$. Reducing, we have

a probable fifth-generation population consisting of 1 heterozygous for three pairs and homozygous for none; 93 heterozygous for two pairs and homozygous for one; 2883 heterozygous for one and homozygous for two; and 28,791 homozygous in all three factor combinations. Of the 32,768 individuals in this generation, 2977, or 9.09 percent, are heterozygous in respect to some characters. Of the 98,304 allelomorphic pairs involved in all the individuals of this generation, 3072, or 3.125 percent, are heterozygous. This is the percentage obtained by halving 100 percent five times. This rate of reduction is shown as line 1 in Fig. 143. As stated before, this is the same for any number of factors. The rate of reduction in the number of individuals heterozygous in some degree, as already shown, differs with varying number of factors and this is demonstrated graphically in the same figure when 1, 5, 10, and 15 factors are involved. Where linkage occurs, this diagrammatic representation will not perfectly apply, but in the end the result will be the same. Heterozygotes are eliminated and homozygotes remain.

Segregation of color in cattle.—The number of different homozygous types which will result from any system of inbreeding depends upon the factor differences at the start and the possibilities of their recombination. This has been shown to be the case with corn. It is the same with all forms of life. If a herd of Shorthorn cattle, consisting of animals with red, roan, and white colors, characteristic of this breed, were closely inbred, there would be finally only reds and whites. The hybrid roan, or mixed red and white, color would disappear. If these Shorthorns were crossed with black Aberdeen-Angus or Galloway and again inbred, there would result blacks, whites with black ears, reds, and whites with red ears. The heterozygous blue roans and red roans, which would be common at first, would in time disappear.

How inbreeding proceeds.—The reduction of 50 percent in heterozygosity in each generation of self-fertilization

applies only when all the individuals are allowed to reproduce and all are equally fertile. In actual practice this is never the case. Inbreeding is always accompanied by selection of one or a few individuals. Usually the most vigorous are taken, and heterozygosity is nearly always an accompaniment of vigor. We should therefore expect the results of inbreeding to depend entirely upon the composi-

TABLE XXXIII

THE THEORETICAL NUMBER AND RATIO OF INDIVIDUALS IN THE CLASSES OF DIFFERENT DEGREES OF HETEROZYGOSITY, AFTER RECOMBINATION, WHEN FIFTEEN MENDELIZING UNITS ARE INVOLVED

Class No.	The total number of individuals in all the possible Mendelian recombinations in F_2 when 15 factors are involved.	Ratio of individuals in the classes with different number of heterozygous and homozygous factors—coefficients $(a+a)^{15}$	The number of factors in respect to which the different classes are:		The total number of heterozygous and homozygous factor pairs in all the individuals in each class:	
			Heterozygous	Homozygous	Heterozygous factor pairs	Homozygous factor pairs
1	32,768	1	15	0	15	0
2	491,520	15	14	1	210	15
3	3,440,640	105	13	2	1,365	210
4	14,909,440	455	12	3	5,460	1,365
5	44,728,320	1365	11	4	15,015	5,460
6	98,402,304	3003	10	5	30,030	15,015
7	164,003,840	5005	9	6	45,045	30,030
8	210,862,080	6435	8	7	51,480	45,045
9	210,862,080	6435	7	8	45,045	51,480
10	164,003,840	5005	6	9	30,030	45,045
11	98,402,304	3003	5	10	15,015	30,030
12	44,728,320	1365	4	11	5,460	15,015
13	14,909,440	455	3	12	1,365	5,460
14	3,440,640	105	2	13	210	1,365
15	491,520	15	1	14	15	210
16	32,768	1	0	15	0	15
16	1,073,741,824	32,768	15	15	245,760	245,760
$n+1$	$(2^n)^2$	2^n	n	n	$\frac{1}{2}(n.2^n)$	$\frac{1}{2}(n.2^n)$

tion of the individuals selected as the progenitors of the subsequent generations. We might choose an individual which was completely heterozygous and get no reduction in vigor or approach to uniformity. On the other hand, it would be possible to pick the ones that were completely

homozygous and thus get a stable and uniform strain right from the start. The chances, however, of doing either of these are very remote where a large number of factors are involved, as is almost always the case. Take, for example, an individual which has 15 heterozygous factor pairs. If these are all independent, that is, show no linkage, the progeny of a self-fertilized parent will range from those which are heterozygous in all and homozygous in none to those which are heterozygous in none and homozygous in all factor pairs. There will be very few which are completely heterozygous or completely homozygous; in fact, there will be only one of each in every 32,768, on the average. The chance of finding either of these two in such numbers is small. The bulk of the offspring will be in the medium grades of heterozygosity as shown in Table XXXIII and Fig. 144. By far the greater number of individuals in this first inbred generation will not be heterozygous in more than ten or less than five pairs. Therefore, it is likely that any individual chosen as the progenitor for the next generation will be about half as heterozygous as its parent, and so on in each subsequent generation until complete homozygosity is ultimately obtained. If 20 instead of 15 factors were involved, only one out of 1,048,576 would be completely fixed in all its characters in the first inbred generation and show no further reduction in size or vigor. The tobacco plant has 24 chromosomes. With a heterozygous factor in each chromosome pair, the progeny of such a hybrid plant would have to number 16,777216 individuals in order to have an even chance of securing, somewhere in the lot, one plant which would be completely homozygous. This number of plants would require over 2000 acres of land, as tobacco is grown in field culture.

Linkage enters as a complicating agency. Factor groupings tend to stay together, so that some lines will be reduced to complete uniformity more slowly than others. On the average, however, the results are the same, as the associated factors, when once broken up, tend to stay in

their new arrangement as firmly as they formerly resisted separation.

Linkage and recombination.—Linkage increases the difficulty of producing individuals in which all the favorable dominant factors are combined. Such individuals, if they

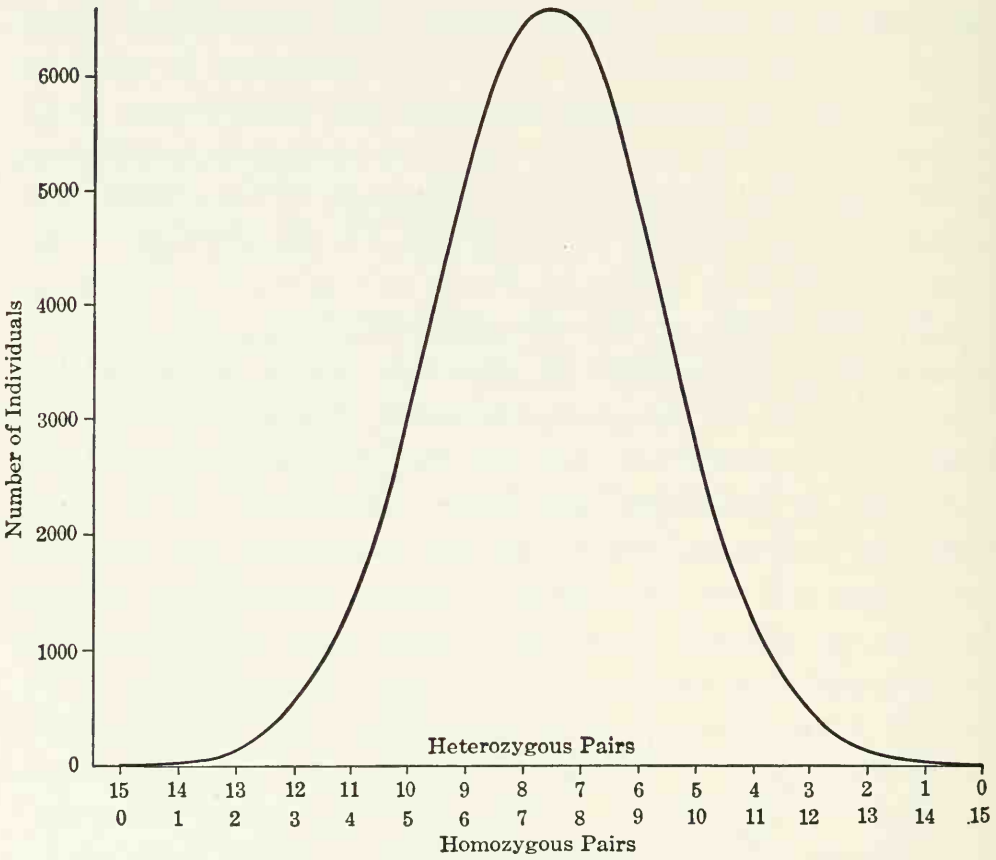


FIG. 144.—Graph showing the theoretical distribution of a self-fertilized organism heterozygous in fifteen allelomorphic pairs plotted from the figures given in Table XXXIII. The bulk of the individuals are in the central area. Any individual selected at random as a progenitor of a self-fertilized line is therefore likely to be about half as heterozygous as its parent. This will continue to be the case, on the average, until homozygosity is obtained.

could be obtained from our present cross-fertilized plants and animals, would be very valuable, as they would show no loss of vigor when inbred and they would be far more uniform than the original stock. Moreover, they would be expected to be larger and stronger than the crossbred race

from which they came, because dominance is seldom complete, and the hidden recessive germplasm carried in practically all cross-fertilized plants and animals, although masked, is never completely counterbalanced, and acts as a restraining influence, preventing maximum development. With a double set of all the best growth factors acting together in one individual, that individual would be the founder of a variety or breed measurably superior to the original heterozygous stock.

This is undoubtedly just what has taken place in the naturally self-fertilized plants and many cross-fertilized species in the wild. Wheat, oats, barley, peas, beans, tomatoes, and tobacco are almost wholly self-fertilized naturally in every generation; yet these plants lack nothing in vigor and productiveness when compared with other crop plants which are usually cross-fertilized. Many wild cross-fertilized species are not reduced by inbreeding. Collins finds that teosinte, a semiwild relative of maize, is not noticeably affected adversely by self-fertilization. The attainment of such combinations among present forms of domesticated animals and cross-fertilized plants is so extremely difficult that we can hardly hope that this will be an important method of improvement until knowledge of the processes of heredity is much more complete than it is now.

Effectiveness of different systems of mating.—Of all the systems of consanguineous mating, self-fertilization is the quickest and surest means of obtaining uniformity and constancy. This is easily understood, from the fact that every homozygous combination must remain homozygous, while the heterozygous combinations are automatically halved. The mating of brother and sister in each generation is the next most effective system. But in this process a homozygous individual may be paired with a heterozygous one and in that way the attainment of complete homozygosity may be delayed. Brother and sister and various systems of cousin and other relationship matings give vary-

ing results, as shown in Fig. 145. On the average, six generations of self-fertilization are more effective than seventeen generations of brother and sister matings in bringing about uniformity and stability.

Terms used to denote different systems of mating.—Livestock breeders have used various terms in an attempt to distinguish between different degrees of inbreeding. Such expressions as in-and-in breeding, line-breeding, interbreeding, and crossbreeding, however, carry no precise meaning. Inbreeding generally refers to the closer kinds of matings, such as brother and sister or parent and offspring,

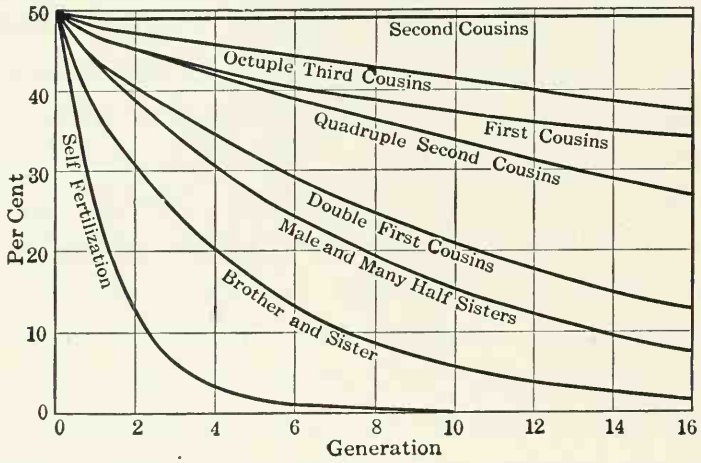


FIG. 145.—The decrease in heterozygosity in successive generations of inbreeding resulting from various systems of mating. (After Wright in U. S. Dept. of Agr. Bull. 1121.)

and in-and-in breeding is the continuation of the same through two or more generations. Line-breeding is used to designate a less intense form of relationship mating. It is also applied to the mating back of the descendants to one sire or dam for as many generations as is possible. This is much practiced in cattle and horse breeding where the individuals are rather long-lived. It is a very effective means of bringing about uniformity, provided the sire or dam used is fixed in its heredity. If the animal which is line-bred to its own descendants is heterozygous, no amount of back-crossing can result in any increase in uniformity of

the progeny, and there will probably be no improvement in any other respect. Interbreeding and crossbreeding are used to denote matings between different families and between different breeds. Outbreeding is a general term to include any mating where the forms united are wholly unrelated as far as there is any evidence.

Inbreeding implies restricted parentage.—Some would limit the use of the term inbreeding to brother and sister or parent and offspring matings, but this is a purely arbitrary

FIG. 146.—The result of inbreeding after crossing. Two inbred strains of maize are shown at the extreme right. The tallest row is their first-generation hybrid, followed by seven successive generations of self-fertilization.

distinction. Obviously, the term inbreeding can be used in a relative sense only. To say that one individual is inbred, and that another is not, is as indefinite as to say that one is short, the other tall. Inbreeding refers only to the way in which individuals are mated together. Underlying all definitions of inbreeding there is the idea of a narrowing of the network of descent, resulting from the bringing together of individuals genetically related to each other in some degree. "The inbred individual possesses fewer different ancestors in some particular generation or generations than

the maximum possible number for that generation or generations," as Pearl well says.

According to the evolutionary conception of descent from a common origin, all individuals must be related in some degree. David Starr Jordan has calculated that every individual of English descent would have had 8598 million living ancestors at the time of the Norman Invasion, if there had been no inbreeding of any degree since that time. It is only necessary to point out that the total population of the British Isles at that time was probably not more than 3 million, to show the amount of inbreeding which has taken place in human stock. Every distinct race, each outstanding breed of domestic animals, and many varieties of plants have resulted from more or less intensive inbreeding.

Mathematical considerations of inbreeding.—There are three distinct phases of the inbreeding problem, as Pearl has pointed out:

1. The system of mating, with regard to the relation of the actual number of ancestors making up the pedigree of an individual to the total possible number.

2. The constitution of each individual with respect to Mendelian unit factors, which results from the continued operation of a given system of mating, which is inbreeding.

3. The physiological effect produced upon the individual by the constitution derived from this system of mating.

The first two phases of the problem are subject to abstract mathematical treatment. The third can be solved only by experimental investigation.

A measure of consanguinity.—In order to compare the intensity of inbreeding produced by different systems of mating, it is necessary to have some measure of the amount of consanguinity. This is done by means of the *coefficient of inbreeding* and *coefficient of relationship*, as devised by Pearl. The first is a measure of the actual number of ancestors compared with the possible number. Any individual in bisexual matings has two parents in the first ancestral gener-

ation, four grandparents in the second ancestral generation, and so on, according to the following symbolical representation:

$$x \longleftrightarrow (1)2 \longleftrightarrow (2)4 \longleftrightarrow (3)8 \longleftrightarrow (4)16 \longleftrightarrow (5)32 \longleftrightarrow (n)2^n,$$

in which the numbers enclosed in parentheses represent the ancestral generations (1 = parents, 2 = grandparents, 3 = great-grandparents, etc.), and the other figures the number

FIG. 147.—The result of inbreeding after crossing. Representative plants from the plots shown in Fig. 146.

of ancestors in that particular generation. In the second or previous generations, the ancestors may not all be different individuals, so that in any generation before the parental the actual number of ancestors may be less than the possible number. For example, in brother and sister mating, any individual, instead of having four different grandparents, has only two. The coefficient of inbreeding, Z, is based upon this difference and is calculated from the formula:

$$Z_n = \frac{100(p_{n+1} - q_{n+1})}{p_{n+1}}$$

where n is each ancestral generation from the individual itself, which is 0, as far back as the pedigree is studied. The term p_{n+1} denotes the maximum *possible* number of different individuals involved in the matings in the $n+1$ generation, and q_{n+1} gives the *actual* number of different individuals involved in these matings. Applying this

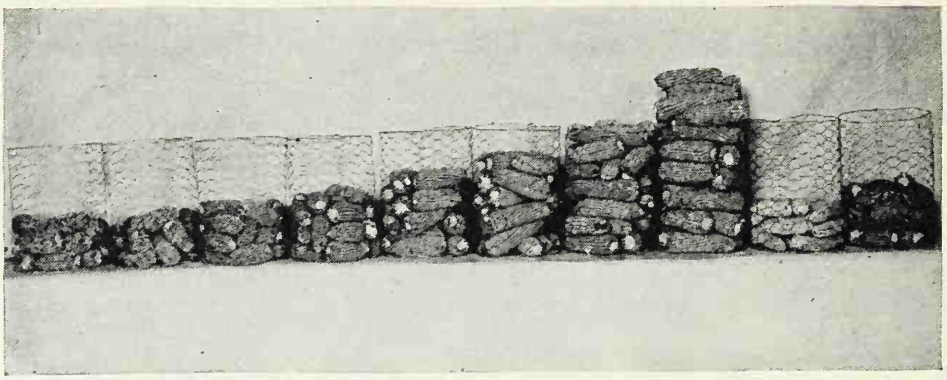


FIG. 148.—The result of inbreeding after crossing. The average production of grain from the plots shown in Fig. 146. From left to right: two inbred strains after ten generations of self-fertilization; their first generation hybrid and the result of seven successive generations of self-fertilization.

formula to continued brother and sister matings we get the coefficients of inbreeding as follows:

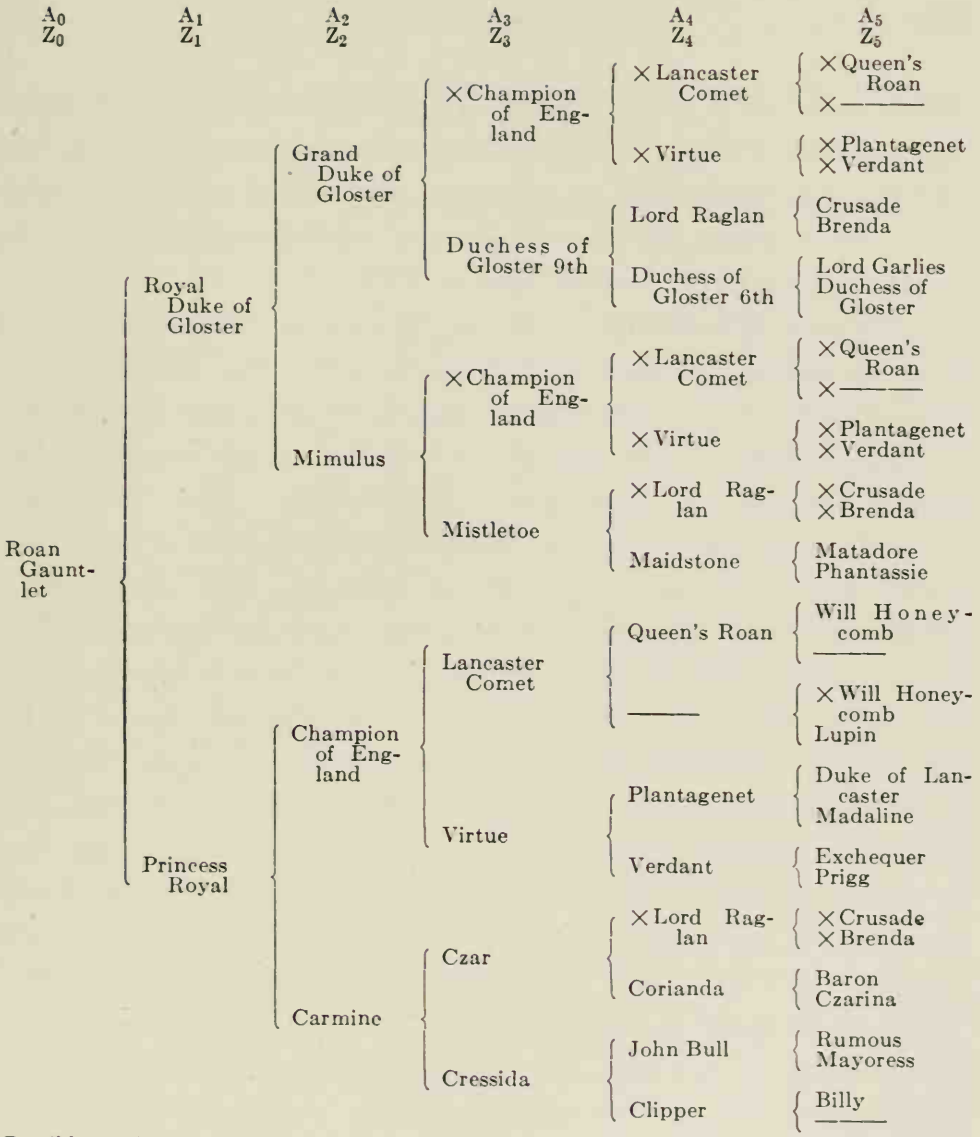
$$Z_0 = \frac{100(2-2)}{2} = 0$$

$$Z_1 = \frac{100(4-2)}{4} = 50$$

$$Z_2 = \frac{100(8-2)}{8} = 75$$

$$Z_3 = \frac{100(16-2)}{16} = 87.5$$

The coefficients obtained are the differences between the possible and actual number of ancestors, expressed as percentage of the former. By plotting these percentages for successive generations, we obtain a curve of inbreeding



Possible no. Ancestors, p = 2	4	8	16	32
Actual no. ancestors, q = 2	4	6	10	19
No. of repeated ancestors 0	0	2	6	13

$$Z_0(A_1) = \frac{100(p_1 - q_1)}{p_1} = \frac{100(2-2)}{2} = 0 \text{ percent}$$

$$Z_1(A_2) = \frac{100(p_2 - q_2)}{p_2} = \frac{100(4-4)}{4} = 0 \text{ percent}$$

$$Z_2(A_3) = \frac{100(p_3 - q_3)}{p_3} = \frac{100(8-6)}{8} = 25 \text{ percent}$$

$$Z_3(A_4) = \frac{100(p_4 - q_4)}{p_4} = \frac{100(16-10)}{16} = 37.5 \text{ percent}$$

$$Z_4(A_5) = \frac{100(p_5 - q_5)}{p_5} = \frac{100(32-19)}{32} = 40.625 \text{ percent}$$

FIG. 149.—Method of calculating the coefficient of inbreeding from the pedigree of Roan Gauntlet. Each name that has already appeared in the same or lower generation is crossed off. When an individual is once crossed off, all of his or her ancestors can be crossed off as far back as the pedigree goes. The percent which the number of repeated ancestors is of the total number of ancestors possible for each generation is the coefficient of inbreeding.

which can be compared with the curves obtained by other systems of mating. Such a comparison is shown in Fig. 145 for the common types of matings, as worked out by Wright. The calculation of the coefficient of inbreeding from an actual pedigree is shown in Fig. 149.

Cross-relationship.—The coefficient of inbreeding alone tells us nothing as to the relation between the different lines of descent. Two individuals may have the same coefficients when considered for any given number of generations, but differ greatly in germinal constitution. The two lines brought together in the immediate production of a particular individual may or may not be related. For example, a closely inbred animal of one breed may be mated with a closely inbred animal of an entirely different breed. The two lines of descent would then be totally unrelated as far as the known pedigrees are concerned, but the resulting individual would have a high coefficient of inbreeding, due to the concentration of ancestry separately in the two parental breeds. Obviously, some measure of the inter-relation of the lines of descent is necessary, and for this reason the coefficient of relationship, K, has been devised. This is essentially the percent of individuals in each of the descending lines which are also represented in the other line. Both constants are necessary to give a complete mathematical estimation of the degree of inbreeding. Usually there is a direct correlation between them; when the coefficient of inbreeding is high the coefficient of relationship will also be high, but in certain cases one may be high and the other zero, as illustrated by Pearl from the pedigrees of two Jersey bulls, as shown on page 345.

The coefficient of relationship, K, is a measure of the inter-relationship, the community of ancestry of the dam and the sire. The coefficient of inbreeding, Z, measures the total relationship, and shows the intensity of inbreeding in the stockman's sense of the word by measuring precisely the proportionate degree to which the actually existent number of different ancestors fails to reach the possible number, and

INBREEDING "Z" AND RELATIONSHIP "(K)" COEFFICIENTS OF TWO JERSEY BULLS

	King Melia Rioter 14th	Blossom's Glorene
A_1 Z_0 (K_1)	0 (0)	0 (0)
A_2 Z_1 (K_2)	25 (0)	0 (0)
A_3 Z_2 (K_3)	25.00 (50.00)	12.50 (0)
A_4 Z_3 (K_4)	37.50 (62.50)	12.50 (0)
A_5 Z_4 (K_5)	50.00 (75.00)	25.00 (0)
A_6 Z_5 (K_6)	71.88 (87.50)	29.69 (0)
A_7 Z_6 (K_7)	81.25 (92.19)	35.94 (0)
A_8 Z_7 (K_8)	90.63 (92.97)	40.23 (0)

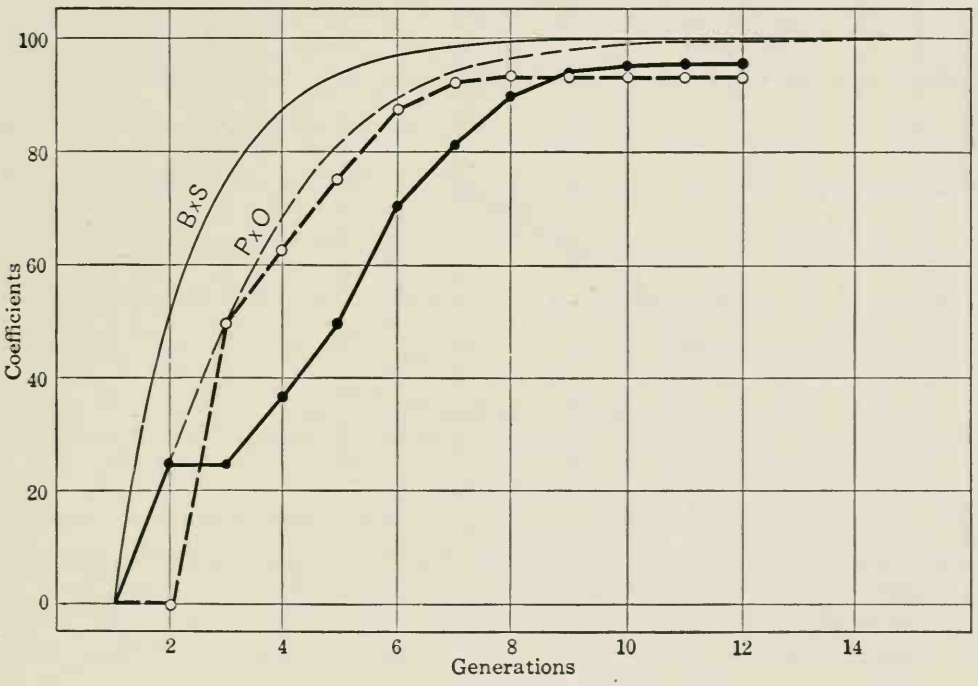


FIG. 150.—Graphs showing the total inbreeding (heavy solid line) and the relationship (heavy broken line) for the Jersey bull, King Melia Rioter XIV. The high degree of inbreeding and relationship between the sire and dam in this case is evident by comparison with the lighter lines, which give the maximum values for continued brother×sister, and parent ×offspring matings. (After Pearl in Maine A. E. S. Bull. 243.)

by specifying the location in the series of the generation under discussion. An examination of the coefficients of inbreeding shows that King Melia Rioter 14th had less than 10 percent of the number of ancestors he might have had in

the eighth ancestral generation, while in the same generation Blossom's Glorene had nearly 60 percent. It is evident that King Melia Rioter 14th is a much more inbred animal than Blossom's Glorene. This is shown graphically in Figs. 150 and 151 where the curves of inbreeding and relationship of King Melia Rioter 14th and Blossom's Glorene are plotted from the figures just given and compared with the curves

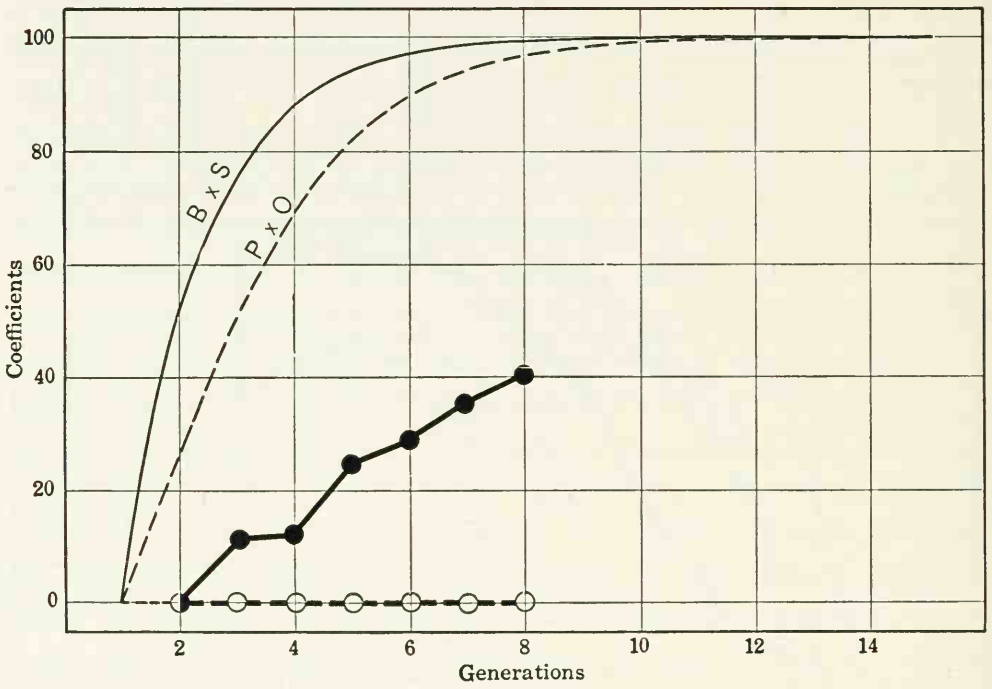


FIG. 151.—Graphs showing the total inbreeding (heavy solid line) and the relationship (heavy broken line) for the Jersey bull, Blossom's Glorene, over a period of eight ancestral generations. Note the low degree of inbreeding and absence of relationship between the sire and dam in this case. Compare with Fig. 150. (After Pearl in Maine A. E. S. Bull. 243.)

of maximum values for brother by sister and parent by offspring matings.

Combining the coefficients of inbreeding.—As a final measure of inbreeding, it is desirable to gather all the coefficients together for a given number of generations in a single term. This is done by Pearl by comparing the area enclosed by the curve of actual inbreeding with the area of the curve of maximum possible inbreeding. This is illustrated in Fig. 152 from the pedigree of Saxton, a Brown

Swiss bull. Saxton is less inbred than the maximum possible amount to an extent which is proportionate to the amount by which the area $T(acd)$ is smaller than the area $M(abd)$. In application, it is sufficiently accurate merely to sum up the coefficients of inbreeding shown by any individual for a given number of generations, and find what percent this figure is of the sum of the coefficients of inbreeding by continued brother and sister mating for the

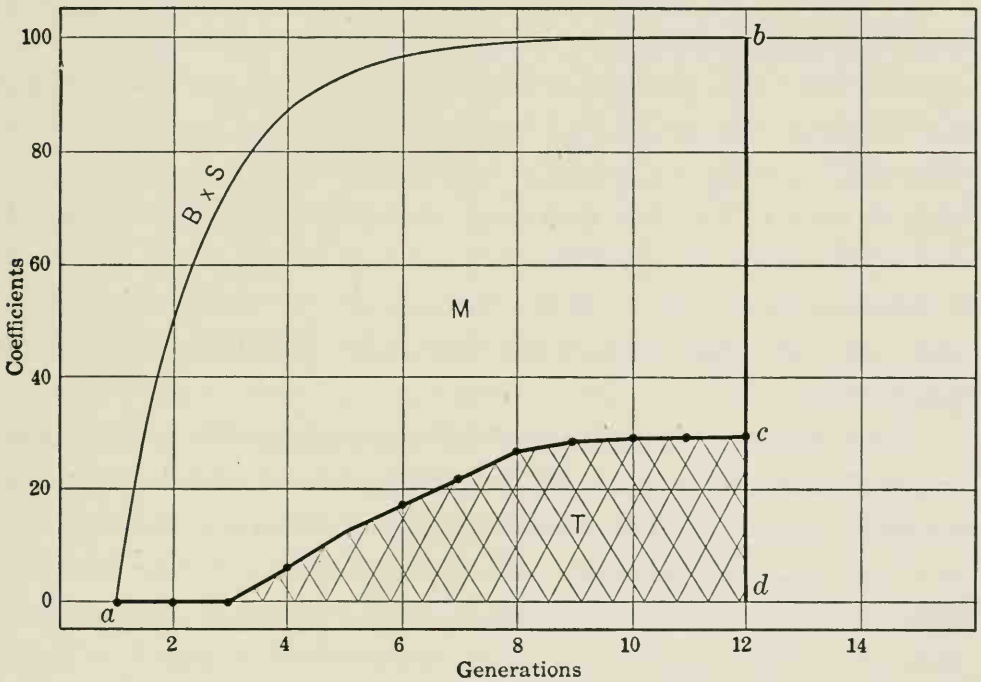


FIG. 152.—Graphs showing the total inbreeding of the Brown Swiss bull, Saxton. The percent which the area *acd* is of the total area *abd* is a single measure of the amount of inbreeding. (After Pearl in the American Naturalist.)

same number of generations. These latter figures are shown in Table XXXIV.

The coefficients of inbreeding for the bull Saxton from the first to the tenth ancestral generation add up to 142.19. From the preceding table, the figure corresponding to the same number of generations of brother by sister mating is 800.1953. By division, this gives the coefficient of total inbreeding as 17.8. One may say, therefore, that Saxton is inbred in ten ancestral generations, taken together, 17.8

TABLE XXXIV

THE INCLUSIVE AREAS OF THE MAXIMUM INBREEDING CURVE OF BROTHER AND SISTER MATING UP TO THE 16TH ANCESTRAL GENERATION OBTAINED FROM THE SUMMATION OF THE COEFFICIENTS OF INBREEDING

Data from Pearl, in *American Naturalist*

Ancestral Generation	Summation of Coefficients	Ancestral Generation	Summation of Coefficients
2	50	10	800.1953
3	125	11	900.0976
4	212.5	12	1000.0488
5	306.25	13	1100.0244
6	403.125	14	1200.0122
7	501.5625	15	1300.0061
8	600.7812	16	1400.0030
9	700.3906		

percent of the maximum amount possible for those generations.

The system of mating not an accurate guide to germinal composition.—The rate of concentration of ancestry, in the progeny as a whole, resulting from different systems of mating has been shown. The composition of the individuals making up these progenies, with respect to the proportion of homozygous and heterozygous factor pairs, is indicated roughly. But it should be understood clearly that one individual whose ancestors have never been closely inbred may be almost completely homozygous in its germinal constitution, while another coming from a rigidly inbred line may be extremely heterozygous, although this is not the usual result. All degrees between these two extremes will be found. Relationship mating does not, therefore, necessarily insure homozygosity and its consequent uniformity and stability. It merely brings about a condition in which chances are enormously increased that such will be the outcome. Any tendency to select vigorous offspring holds off this approach to complete reduction.

The effect upon any particular individual depends upon

the hereditary factors which have been allotted to it. This is wholly a matter of chance. Therefore, while one can gain some idea of the composition of an individual by a careful consideration of the composition of the generation to which it belongs, no one can tell exactly what its composition will be until it is actually produced and tested. What the effect of the hereditary factors handed out to each individual will be, must also be determined by actual observation.

The one demonstrable effect of inbreeding.—In conclusion, it can be said that inbreeding has but one demonstrable effect on organisms subjected to its action—the sorting out of pure-breeding homozygous types. The differences exhibited by the resulting inbred types depend directly upon the number of heterozygous hereditary factors present in the individuals with which the process is begun; it is likely, therefore, to vary directly with the amount of crossbreeding experienced by their immediate ancestors. The rapidity of the sorting out of homozygous types is closely connected with the intensity of inbreeding.

Summary.—Let us take the case of maize as an illustration of this principle. Maize is one of the most variable of cultivated plants, and it is almost completely cross-pollinated in every generation under natural field conditions. The individuals making up any commercial variety are each and every one heterozygous for a large number of hereditary factors—a condition which is kept up by continual crossing and recrossing. When such a variety is inbred there is an automatic sorting out of homozygous combinations following simple mathematical laws. With self-fertilization, uniformity and stability are reached after a relatively small number of generations; if a less intensive system of inbreeding is followed, the result is the same, but it is attained more slowly. During this process, before stabilization is reached, there is a reduction in size, vigor, and productiveness, following somewhat roughly the reduction in degree of heterozygosity. The decrease in vigor of the population as a whole in

each generation, up to a certain point, is associated with the isolation of individuals more homozygous than their parents.

Any particular individual may be vigorous or weak, fertile or sterile, normal or monstrous, good, bad, or indifferent, depending wholly upon the combination of characters allotted to it. Many of these characters will be recessives or combinations of recessives which were never or seldom seen in the original stock before being inbred, because they were hidden by their dominant mates. These recessives are the " corrupt fruit " which give the bad name to inbreeding, for they are often, very often, undesirable characteristics.

The homozygous inbred strains, after stability has been reached, are quite comparable to naturally self-fertilized species, provided they have passed as rigorous selection as the latter have had to undergo by reason of natural competition. Darwin, as well as others, found that artificial self-pollination causes no reduction in such plants as tobacco, peas, and beans, where self-fertilization is the general rule.

We see, therefore, that the immediate results of inbreeding are sometimes injurious, or even disastrous, when we recall the reduction to over one-half or one-third in production of grain and a corresponding decrease in size of plant and rate of growth in maize. Particularly with swine and poultry, and sometimes with other domesticated animals, there is often a pronounced reduction in fertility, constitutional strength, and speed of development. With other organisms the results are not so bad; and in some cases, especially when selection has been made, no evil effects result. In fact, there may be an actual improvement, as has been found with rats.

These are facts which, for the most part, have long been known. What is wanted is an answer to the question, " Is inbreeding injurious merely by reason of the resulting consanguinity? " Is close mating, in itself, injurious? Backed by two decades of genetic investigation, we can answer positively, " No! " *The only injury which may proceed from inbreeding comes from the inheritance received.*

The constitution of the individuals resulting from a process of inbreeding depends upon the chance allotment of characters preëxisting in the stock before inbreeding was commenced. If undesirable characters are shown after inbreeding, it is only because they already existed in the stock and were able to persist for generations under the protection of more favorable characters which dominated them and kept them from sight. The powerful hand of natural selection was thus stayed, until inbreeding tore aside the mask and the unfavorable characters were shown up in all their weaknesses, to stand or fall on their own merits.

If evil is brought to light, inbreeding is no more to be blamed than the detective who unearths a crime. Instead of being condemned, it should be commended. After continued inbreeding, a previously crossbred stock has been purified and rid of abnormalities, monstrosities, and serious weaknesses of all kinds. Only those characters which are favorable, or at least not definitely harmful to the organism, can remain. *Nothing of value need necessarily be lost.* Those characters which have survived this " day of judgment " can then be estimated according to their true worth. Only by some system of inbreeding can thorough selection be carried on with crossbred animals. Self-fertilization is the simplest and most effective means by which the heredity can be controlled through the pollen parent, as well as the seed parent, in plants. If vigor is lost in the process, it can be immediately regained by suitable crossing. Not only is the full vigor of the original stock restored, but it may even be increased, through the elimination of many unfavorable characters. If this increased vigor can be utilized in the first generation, or if it can be fixed by vegetative propagation so that it is not lost in the multiplication of individuals, or if a new variety or breed can be re-created from the purified inbred strains of the old stock, then inbreeding is not only not injurious, but is highly beneficial and should be given its rightful valuation as an actual means of plant and animal improvement.

CHAPTER XIII

STERILITY

The ability of the plant or animal to reproduce itself in large numbers is of the utmost importance in domestication. The seeds and accessory parts are the economic goods for which plants are largely grown. In animals, eggs and milk are valuable products which are directly and indirectly connected with the reproductive process. Whatever may be the uses to which animals and plants are put, the facility with which they are increased in numbers largely determines their suitability for domestication and continuation under artificial conditions.

Reproduction under natural and artificial conditions.—The ability to reproduce is naturally one of the first things for which domesticated forms have been selected. In most cases, a marked increase over the primitive conditions of reproduction has been obtained. The wild jungle fowl lays about two dozen eggs a year, which seems trifling when compared with the two hundred and more of the well-bred and well-fed barnyard hen. Wild sheep and mountain goats seldom have more than one young each year, whereas the many farm breeds frequently produce twins and sometimes triplets.

Plants, too, have been much changed in this respect, although the alteration is largely in size of seed rather than in numbers. This greater size gives the young plants a better start and makes their cultivation easier. Numbers, also, are not lacking in many plants. The larger varieties of corn reproduce themselves a thousandfold. A cultivated tobacco plant easily makes one hundred thousand seeds, enough to plant about seven acres, if all are sown.

This increased production of domesticated animals and plants is due in part to the care and feed given them, and consequently to their better opportunity to grow; yet the differences between plants and animals in the wild and under domestication are to a large extent fixed in the germplasm. Wild types will not respond to good care to the same extent as will the tame races. While the increase in reproductive ability is appreciable, there is room for much improvement. It is stated by Marshall that horse raising in England is handicapped by the failure of 40 percent of the mares to breed. Fifteen percent of cattle, according to Heape, are unable to bear young. Sheep and swine show less loss, but sterility with them is no small matter. With the commercial methods of poultry raising now employed, nearly 50 percent of the eggs fail to hatch. Although artificial incubation is less efficient than natural hatching, the loss is great even with the latter method. Influences outside of the egg have a great deal to do with hatchability; yet hereditary factors within the egg determine the outcome to an appreciable extent.

One of the greatest losses in agriculture is due to the failure to secure a satisfactory stand of plants in the field. The conditions which determine good germination are to a large extent beyond the control of the seed, both before and after planting, but part of the poor germination is due to physiological weaknesses and actual germinal sterility. In both animals and plants, an increase in fertility is an important means of improvement.

Definition of terms.—Before taking up a consideration of the manifestations of sterility, it is necessary to have certain terms defined. **Fecundity,** in common usage, applies to the potential reproductive capacity. It is a measure of the ability to form mature ova and spermatozoa. **Fertility** signifies the ability to bring forth living young. In bisexual reproduction, fertility is dependent upon two individuals, which may not be equal in fecundity. The potential reproductive capacity of one is limited by that of

the other. **Productiveness** is used in a special sense as a term which sums up the entire ability of the plant or animal to propagate its kind. When used in this way, it is practically synonymous with fertility, but is more inclusive, as the ability to produce offspring is governed by the health and vigor of the organism as well as by its potential reproductive capacity.

The agencies which limit productiveness are numerous and diverse in their effect. Essentially they fall into two classes: first, those which are environmental, largely external to the organism, and beyond its control; second, those which are germinal, internal, and peculiar to the organism.

The environmental causes of sterility are so numerous and so complex that no complete treatment of this subject can be given here. The most important considerations come under the headings of nutrition, light relation, mode of life, and disease.

Nutrition.—Sterility may be induced by either a deficiency or an excess of food. Obviously, a plant or animal must have sufficient nourishment or it can not reproduce properly. However, it is not enough that food be supplied in sufficient quantities; it must also be properly balanced. Kraus and Kraybill, working with tomatoes, find that fertility is dependent upon a suitable relation between mineral salts and the starches and sugars manufactured by the plants. They give these general rules for the relation of nitrates, carbohydrates, and moisture within the plant to fruitfulness:

1. Though there be present an abundance of moisture and mineral nutrients, including nitrates, yet without an available carbohydrate supply, vegetation is weakened and the plants are nonfruitful.

2. An abundance of moisture and mineral nutrients, especially nitrates, coupled with an available carbohydrate supply, makes for increased vegetation, barrenness, and sterility.

3. A relative decrease in nitrates in proportion to the carbohydrates makes for an accumulation of the latter; and also for fruitfulness, fertility, and lessened vegetation.

4. A further reduction of nitrates without inhibiting a possible increase of carbohydrates makes for a suppression both of vegetation and fruitfulness.

These are not the only nutritive ingredients which are concerned with fertility but simply show the importance of proper balance. This is also true of animals. Osborne and Mendel, at the Connecticut Station, have grown rats

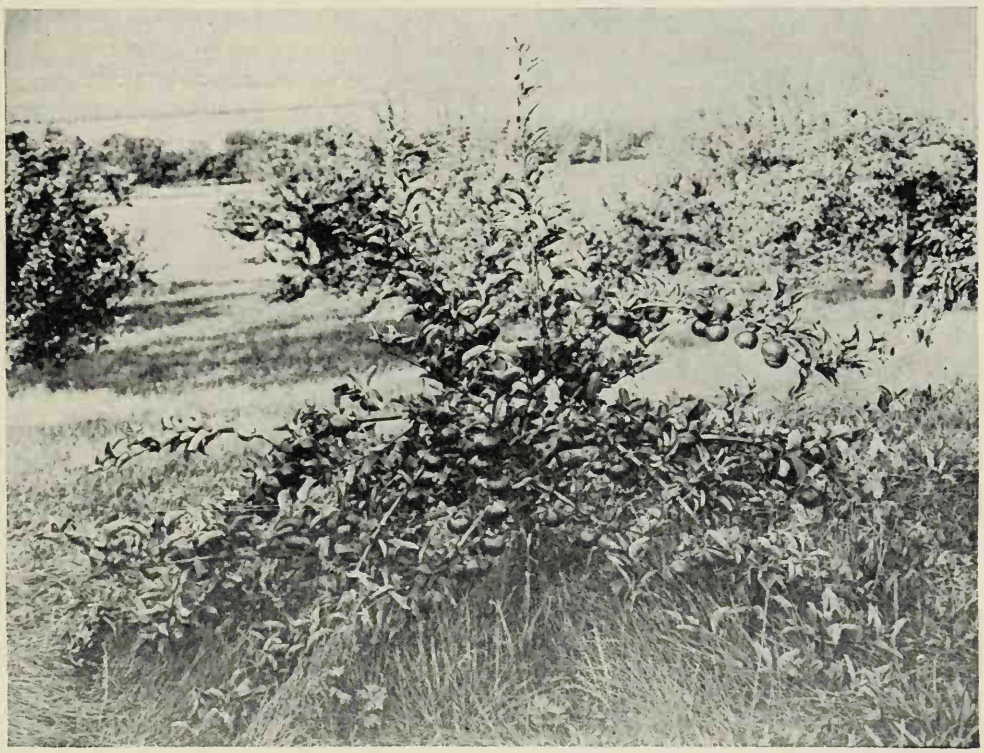


FIG. 153.—Apple tree grown in sod, four years from planting, bearing a full crop.

on restricted diets, to full size and at the usual rate of growth. While these were vigorous and apparently normal in every way, the great majority were sterile, apparently because some essential substance, which has not yet been identified, was lacking in their food. The control of the food over fertility is well shown among the bees and other social insects, where the queen is the only egg-laying female in the colony. The only difference betwen a queen and a sterile worker, as far as can be determined, is in the kind of food

supplied during development. This is demonstrated when the queen and the larvae which are destined to be queens are removed from a colony. The workers enlarge an ordinary worker cell and, by giving the larva therein the food that ordinarily would have been given to the queen larva, enable an otherwise sterile insect to become an egg-layer.

An excess of food is also prejudicial to full fertility. Fruit trees that are liberally fertilized and cultivated, in such a manner as to stimulate vegetative growth, are notoriously slow in coming into bearing. If blossoms are formed, these are dropped off shortly after pollination. Trees that are grown slowly will blossom and set fruit at an early age after planting. With animals, an excess of food, above the amount necessary to maintain a thrifty condition in breeding stock, makes fertilization more difficult and often reduces the number of young produced.

Light relation.—As brought out in Chapter VII, a pronounced environmental effect upon fertility is shown by the alteration of relative length of day and night. Plants which normally make a rank vegetative growth and produce few seeds or none under certain seasonal conditions, when subjected to shorter or longer periods of sunlight, check their vegetative growth, blossom, and set seed abundantly. Teosinte, a semi-tropical grass related to maize, when grown in the North makes a large growth of stalks and leaves but does not usually flower. If the plants are grown in the greenhouse during the winter, when the days are shorter, they make a smaller growth, but flower and produce seed freely. The same result can be secured in the open during the summer, by keeping the plants dark during a part of the day and exposing them for a period equal to a day during the winter. The indeterminate type of tobacco, which has been described in Chapter VII as an example of mutation, differs from the normal plants in its reaction to light conditions. Instead of making a definite number of leaves, ranging from 20 to 30 in most varieties of tobacco,

the plants keep on growing until killed by frost in the fall, without any indication of blossoming, and grow from 12 to 15 feet high, about twice the height of ordinary tobacco in the open. These abnormal plants, when grown in the greenhouse during the winter, behave like normal plants and set seed freely. Such plants can also be grown in the tropics during the winter, where, on account of the shorter day, they will produce seed. This fact is taken advantage of in producing seed of this type in large quantities. Some

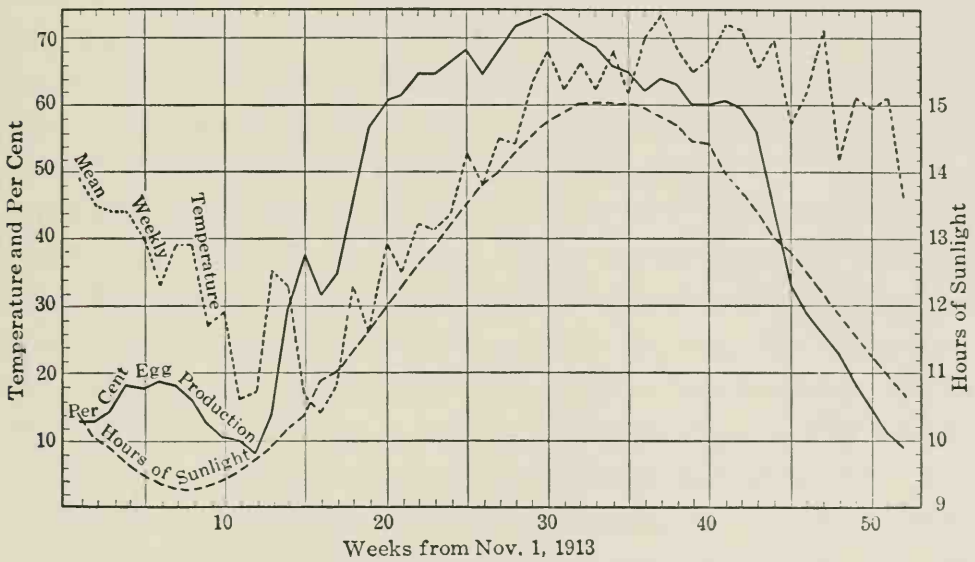


FIG. 154.—Showing graphically the relation between egg production and the temperature and period of daylight. (After Lippincott, based on data from Card in "Poultry Production," courtesy of Lea & Febiger.)

plants are adapted to a short period of daylight, others to a longer period. Whatever the optimum conditions are for any particular species or variety, the results obtained by Garner and Allard show the importance of the proper adjustment of the plants to these conditions. If the plants are not properly adapted, this is shown most noticeably in the effect upon the reproductive process.

Effect of artificial lighting upon egg production.—The light relation in plants probably determines the amount of carbohydrate manufacture, and the ratio of this to the moisture and mineral salts controls vegetative and repro-

ductive processes. Egg laying in poultry is noticeably stimulated by artificial lighting. The effect is so marked that lengthening the day during the winter months is coming to be a well-recognized practice in poultry husbandry. The relation of the daily length of sunlight and temperature to egg production is shown clearly in Fig. 154. The effect of artificial lighting is demonstrated graphically in Fig. 155. The usual explanation of this effect is that

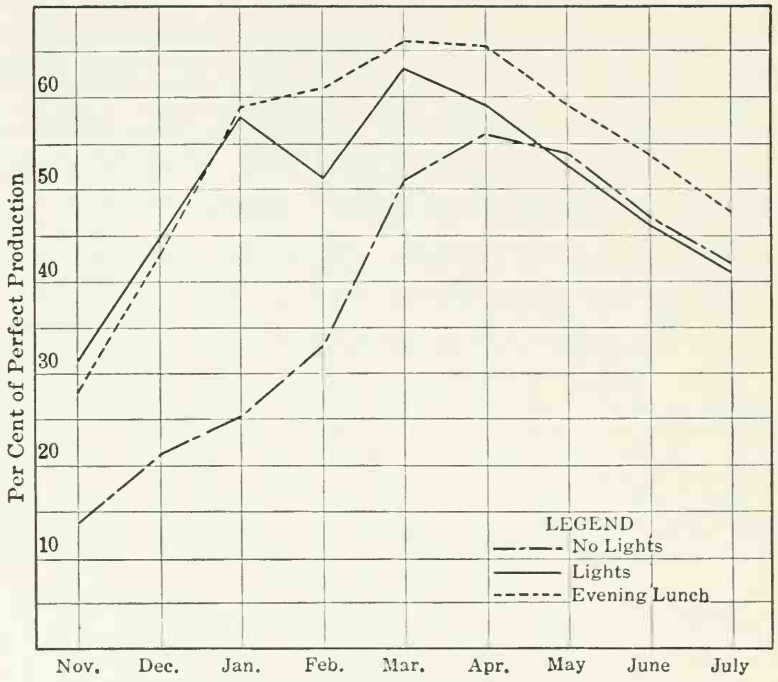


FIG. 155.—Showing graphically the effect of artificial lighting upon egg production. (After Lippincott, based on data by Lewis in "Poultry Production," courtesy of Lea & Febiger.)

the extended period of light reduces the intervals between feedings and permits the hens to consume more food. It may be that this is the only factor involved; yet the similarity of this effect on animals to the effect upon plants is apparent, and there may be some more fundamental physiological effect in common. The wild progenitors of the domestic hen lived in the tropics, where the day, during the winter and early spring, is longer than it is in the North.

Wild animals in captivity are often completely sterile

or at least are very shy breeders. This is probably due to a number of varied causes. One of the chief factors is a radical change and restriction in variety of diet, with the probable elimination of essential food substances. The effect is also partly psychological, ensuing from forced restraint. Whatever the explanation may be, the fact is clear that a radical change of environment may bring about a failure to reproduce.

Disease is one of the most important non-hereditary causes of sterility among domesticated animals. Contagious abortion is an infectious malady of cattle, which annually takes an enormous toll from the livestock industry. The organism which is responsible for the disease is transferred from one animal to another by contact, but the offspring from diseased cows are not usually infected at birth. With the bacterial disease, white diarrhea, in poultry infection, starts in the egg before it is laid, and so is transmitted from generation to generation like an inherited character. The effect of this disease upon vigor is so marked that it results in a large decrease in productiveness.

Many other pathological conditions interfere with full fertility. Frequently these are amenable to treatment. Accurate diagnosis is the first essential, and when this is followed by proper treatment much loss can be prevented. Bad care of breeding animals is responsible for many cases of abortion. For a more extended discussion of the effects of disease and improper treatment upon the fertility of animals from the breeder's standpoint, the reader is referred to some such book as Winter's "Animal Breeding."[1] It is sufficient to say here that disease, physiological weaknesses and anatomical malformations, while often aggravated by the lack of proper care given to animals, is an indication of poor heredity, and all cases of this kind should be carefully considered before using such animals for breeding purposes.

Classification of inherited sterility.—The external influences of the environment upon fertility are not sharply

[1] John Wiley & Sons, Inc.

defined and in their effects range from full fertility to complete sterility. The internal factors controlling reproduction, which have their basis in the germplasm, act in a more definite manner. Hereditary sterility can be grouped in two main classes. There are cases in which the organism is fully developed and functionally normal in every way, except that fertilization can not take place in certain matings but is easily brought about in other combinations. This type of sterility is known technically as **incompatibility.** In another series of instances, organisms are not normally developed in respect to their reproductive organs and are unable to produce viable germ cells, or the embryos after fertilization may be incapable of development. This type of sterility, which may be manifested in these different ways, is called **impotence.**

FIG. 156.—Sweet cherry in bloom. All of the flowers were self-pollinated except those on the lower branch on the left, which were pollinated by a different variety. (After Sutton in Jour. Genetics.)

Sterility from incompatibility results when organisms are alike with respect to particular sterility factors, and also when they are germinally too dissimilar. The first of these two types of incompatibility is confined almost entirely to plants and occurs commonly in some families and not in others. The second type is illustrated by animals and plants everywhere, by different species or genera which can not be

cross-fertilized with each other because their genetic differences are too great.

Self-sterility.—The first type of incompatibility, due to germinal similarity, is shown by many varieties of cultivated fruits, which are self-sterile; that is, the plants are unable to fertilize their flowers and set fruit with their own pollen. Unless pollen is supplied by some compatible variety, the trees are entirely barren or only partially fruitful. This pollen, which is unable to fertilize the flowers of the same plant or clonal variety which produced it, is fully capable of functioning on other plants of a different variety. Two plants may be entirely self-sterile, but reciprocally fertile, whichever way the pollination is made. There is, therefore, no abnormality in development but merely a limitation in functioning.

FIG. 157.—The same tree as in Fig. 156, taken from opposite side. Only the cross-pollinated flowers have set fruit. (After Sutton in Jour. Genetics.)

Trees which fail to set fruit with their own pollen.—This phenomenon is commonly observed in sweet cherries, plums, almonds, apples, pears, bramble berries, and grapes. Such plants may be perfectly healthy and in a good growing condition and flower abundantly, yet still fail to set fruit unless suitable pollen is available. Not all varieties of these fruits behave in this way, and some kinds of fruit are never or rarely self-sterile. Sour

cherries and peaches are not usually dependent upon cross-pollination in order to fruit. Many self-fertile varieties are benefited by cross-pollination, which increases the size and number of fruits.

Effects of pollination on fruit.—Gowen, from data obtained at the Maine Station, finds that the seeds in cross-fertilized Ben Davis apples are larger and more numerous than in self-fertilized fruits of the same variety; and since the seeds stimulate the development of accessory parts, it is to be expected that the size of the fruit, and possibly the quality to a slight extent, is favorably affected by crossing. This beneficial result varies with different crosses. According to the Maine Station results, the Alderman variety increased the size of Rome Beauty apples 27.8 percent by crossing as compared to selfing. Cross-fertilized York Imperial apples were larger by 42.7 percent. On the other hand, Wagener was reduced 17.3 percent in size by crossing.

Pollen from dissimilar varieties does not alter the character of the fruit. Wicks tested Ben Davis, Grimes, Jonathan, and Winesap varieties at the Arkansas Station, and found no appreciable alteration in color, size, or quality. The varietal characteristics are maintained irrespective of the kind of pollen used. The edible part of the fruit of the apple develops from maternal tissue and shows no xenia effect, as in the endosperm of corn which results from fertilization in the same way that the embryo does. In general, therefore, it is true that a Rhode Island Greening will be just as green when pollinated by Grimes Golden as by Red Astrachan. If size and quality are influenced, it is an indirect effect from heterosis in the cross-fertilized seeds. Better quality, if it is secured at all, may result as easily from cross-pollination with a small and insipid variety as with a large high-quality variety.

Source of pollen.—When self-sterility of this type occurs, it makes no difference whether the pollen comes from the same flower, from different flowers on the same tree, or

from different trees of the same clonal variety, as Gowen shows in Table XXXV. The number of fruits set is proportionally the same, irrespective of the source of the pollen, as long as it has the same germinal composition;

TABLE XXXV

THE RESULT OF POLLINATING APPLE FLOWERS WITH POLLEN FROM VARIOUS SOURCES WITHIN THE SAME VARIETY

Data from Gowen, in Maine A. E. S. Bull. 287

Variety	Flower Cluster Bagged and Left		Pollinated with Pollen of Same Tree		Pollinated with Pollen of different Tree of Same Variety	
	Fruit Matured	No Fruit	Fruit Matured	No Fruit	Fruit Matured	No Fruit
Baldwin	2	11	3	22	..	2
Ben Davis	..	65	..	229	..	26
Crab	..	3	..	8	..	..
Duchess	..	..	1	3	..	..
Early Harvest	..	6	..	7	..	..
Golden Russett	..	15	..	46	..	6
Hurlbert Sweet	..	5	..	10	..	..
McIntosh Red	..	16	..	12	..	..
Northern Spy	..	1	..	34	1	3
Red Astrachan	..	..	..	4	..	..
Rhode Island Greening	..	2	..	10	..	2
Wealthy	1	..	..	..	..	..
Percent fruitful	2.36		1.03		2.50	

and reciprocal pollinations, in general, behave alike. This shows clearly that this type of sterility is inherent in the plants themselves and is not due to environmental causes, although the degree of its expression may be modified somewhat by external influences.

Extent of self-sterility.—Out of 119 varieties of apples tested at the Maine Station, only 42 set fruit when self-

pollinated. Of these only 15 produced fruit of marketable size and quality. At the John Innes Horticultural Institute in England, it was found that 8 out of 34 varieties of apples tested were self-sterile, as were also 16 out of 39 varieties of plums, and 17 out of 22 varieties of sweet cherries. This type of sterility occurs in many plants. It has been found that about 100 different species, scattered among some 50 plant families, show this self-incompatibility. Among cultivated forms, many of the flowering bulbous plants, such as amaryllis, gladiolus, and hippeastrum, behave in this way. The passion flower, carnation, campanula, orchid, poppy, mallow, cinerarea, mignonette, primrose, corydalis, sunflower, chicory, dahlia, and some species of snapdragon are notoriously self-sterile. Many species of cruciferous plants and members of the lily family show the same phenomenon. Rye is outstanding among cereals as being incapable of setting seed freely with its own pollen.

Darwin's experiments with mignonette.—Darwin tested a number of self-sterile plants of mignonette and found that all cross-pollinations were fertile. Arguing from the fact that no two plants are exactly alike in external structure, he assumed that germinal differences always accompanied differences in external appearance, and came to the conclusion that unlikeness in germinal constitution, however slight, was sufficient to bring about mutual affinity of the sexual elements. Consequently, he thought that every self-sterile plant would be fertile when crossed with any other plant of the same species. In other words, "any lock would open to every key but its own."

Cross-sterility.—This has not been found to be the case always, as there are definite instances of cross-sterility as well as self-sterility. East and Park have made a careful study of this problem. Working with various species of tobacco, they have found that incompatibility in sexual fusion is inherited and is determined by definite combinations of transmissible factors, which are relatively little influenced by the external features of the plant. A normally

self-sterile plant may, however, show slight fertility late in the season when the plants are growing slowly. The self-ferilized seeds so produced give plants which are completely self-sterile the next year under normal growing conditions. Several generations of self-sterile plants, self-fertilized in this way by taking advantage of the end-season pseudo-fertility, showed no increase in fertility. The same plants which produced seed in the fall, when carried over the winter in the greenhouse, became completely self-sterile the following season when growing vigorously. This non-hereditary fluctuation in fertility is apparently more pronounced in other species. Many self-sterile fruit trees will set a small crop when self-pollinated, but these fruits are seldom fully developed. Stout, at the New York Botanical Garden, finds with chicory, cabbage, and other plants that there is a rather marked range in seed production. Incompatibility and flower abortion are both common in Chinese cabbage and are governed by the condition of the plant and by the season, as shown in Fig. 159.

FIG. 158.—Different branches on this plum tree were pollinated by four different varieties, only one of which was able to set a full crop. (After Sutton in Jour. Genetics.)

Incompatibility in tobacco.—Tobacco is expecially favorable material in which to study this problem, as the germinal factors are less influenced by external conditions. With the underlying genetic facts made clear, it is easier to investigate the complex manifestations of sterility in other

organisms. East and Park in their studies employed a number of tobacco species, but their main investigations

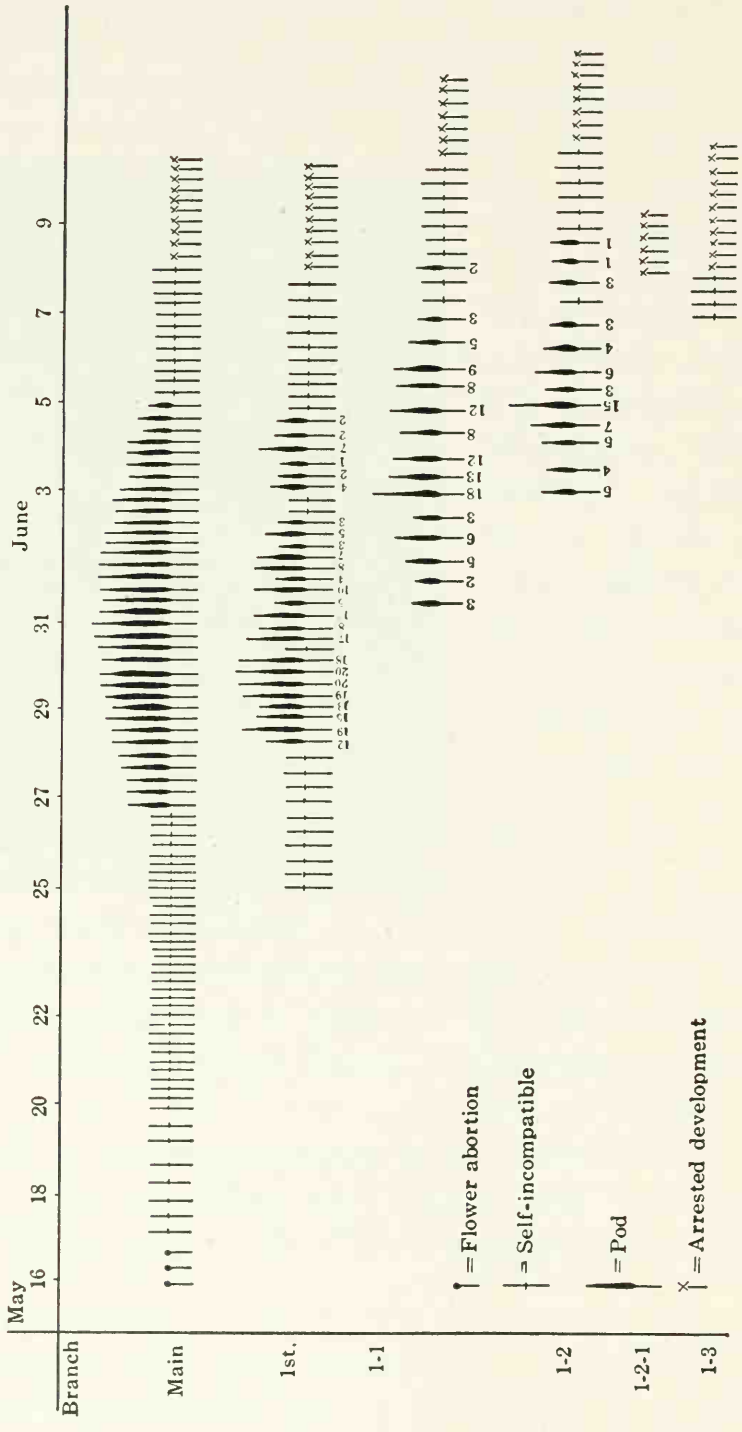


FIG. 159.—Chart showing the distribution in Chinese cabbage, according to time of blooming, of flower abortion, self-incompatibility, arrested development on the main branch and on the uppermost lateral with all its laterals; relative sizes of pods indicated and the number of seeds per pod given for all but the main branch. (After Stout in Botanical Gazette.)

were confined to crosses of *Nicotiana Forgetiana* and *N. alata*. Both species were found to be completely non-

seed-producing when self-pollinated, with the exception, as already noted, that late in the season some partially filled capsules were obtained. As long as inter-pollination took place between different plants, seed was formed abundantly.

Plants used as males

Plants used as females	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	S		F					F			F	F								
2		S									F	F	F							F
3	F		S			F		F			F	F			F		F			
4				S				F			F	F								
5	F				S		F	F	F	F	F	F	F	F	F	F	F	F	F	F
6				F		S		F			F		F	F			F			
7			F				S				F				F		F			
8	F		F	F		F	F	S		F	F	F	F	F	F	F	F			
9				F				F	S			F		F						
10					F			F		S	F	F	S	F	F	F	F			
11					?	F		F		F	S	S	F	F			F			
12			F		F					F	S	S	F	F	F	F	F	F	F	F
13								F			F	F	S		F		F			
14			F		?			F	F			F		S			F			
15					F			F			F	F			S					
16					F					F	F	F		F		S		F	F	
17					F					F	F	F	F		F		S			
18					F		F	F			F	F						S	F	
19			F		F			F						F			F	F	S	
20					?			F					F							S

FIG. 160.—The result of self and cross-pollinations between individual plants in the second generation of a cross between *N. Forgetiana* by *N. alata*. (After East and Park in Genetics.)

The first-generation hybrid plants, produced by pollinating *N. alata* by *N. Forgetiana*, were vigorous and taller by 25 percent than the average of the parents. They were extremely uniform in size and color of flowers. A large number of plants of this generation were examined and

found to have well-developed pollen, but all were self-sterile and produced no seed unless cross-pollinated.

Six hand-pollinations between sister plants gave well-filled capsules. From this seed nearly a thousand plants were grown, which were extremely variable in all their

Plants used as females	Plants used as males																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	S		F	S	F			F	F	F	F	F	F	F	F	F	F			
2	F	S	F	S	S				F		F	F	F	F	F	S	S	F	F	S
3			S	F	F			F	F	S	S									
4																				
5													F							
6	F					S	F	F	F	F	F	F	F							F
7	F	F	S	S	F		S	F	S	S	S									
8					F			S	F	F										
9		F			S				S	F	F	F	F	F						
10			S		S					S										
11											S									
12			F		F		F	S	F	F	F	S	F							
13			S										S							
14			F		F	S	F	F	F	F	F	F	F	S						
15			F		F	S	F	F	F	F	F	F	F	S	S	F				
16			F		F	F	F	F	S	F	F	F	F	F	F	S	F	F	F	S
17			F		F	F	F	S		F	S	S	F	F	F	F	S			
18		F	S		F	F	S	F	F	S	S	F	S	F	F		F	S	F	
19			F		S	F	F	F		F	F	F	F	F	F		F		S	S
20																				

FIG. 161.—The result of self- and cross-pollinations between individual plants in the fifth generation from the same cross as in Fig. 160. (After East and Park in Genetics.)

characters. Twenty plants were self-pollinated and inter-pollinated with each other in nearly all possible combinations. From two to ten pollinations were made in each case, so that their success or failure in developing seed was definitely established. The results are given in Fig. 160,

showing the particular combinations which were fertile and those which were sterile. All the self-pollinations failed to set seed. Of the inter-pollinations, 3 were clearly sterile and 3 more were questionable. The remaining 123 inter-pollinations were all fertile.

Twenty-nine of these fertile capsules were sown, and from 50 to 150 plants of each were set in the field. All proved to be self-sterile. Twelve plants from two of these families were inter-crossed, with the result that 7 combinations out of the 132 possible cross-pollinations were sterile. The majority of those tested were cross-fertile.

Increase in amount of cross-sterility.—Similar tests were carried out each year up to the fifth generation. The results after five successive sib matings, within the family, are shown in Fig. 161. Note the more frequent occurrence of cross-sterility in this generation than in the second, as shown in Fig. 160. It was found that the total amount of sterility increased markedly from the second to the fifth generation, although the last generation was not quite as high in this respect as the fourth, possibly because the numbers tested were too small to give a fully representative result. The actual figures stand in the relation of 14.4, 19.1, 26.2, and 22.2 percent sterile combinations for the four generations. The close inbreeding resulting from brother and sister mating brought about a simplification of the germplasm, such that there were fewer factor differences in the fifth generation than in the second.

A Mendelian interpretation of self-sterility.—This fact indicated the possibility of a Mendelian interpretation of this type of sterility. It was found that the plants of the last generation could be put into five classes: A, B, C, D, and E, such that all the plants of any one class were both self-sterile and sterile with any other individuals of the same class, but fertile with every individual of every other class. The actual results obtained are shown in Table XXXVI. Several exceptions are shown in bold-face type. These are believed to be due to accidental failure in pollina-

TABLE XXXVI

PLANTS OF THE FIFTH GENERATION OF A CROSS OF N. FORGETIANA×N. ALATA, GROUPED IN ACCORDANCE WITH THEIR BEHAVIOR IN INTERCROSSES

Data from East and Park, in *Genetics*

Group	Ped. No.	Number of Cases Fertile Within Group					Number of Cases Sterile Within Group				
		A	B	C	D	E	A	B	C	D	E
A	3	0	5	2	3	1	5	0	0	0	0
	7	0	4	3	3	1	4	1?	0	0	0
	10	0	3	3	3	1	3	1?	0	0	0
	11	0	4	3	1	1	3	1	0	0	0
	13	0	5	3	2	1	2	0	0	0	0
	18	0	5	3	3	–	5	0	0	0	–
B	2	5	2	2	1	1	0	3	0	1	0
	5	4	1	2	3	1	1?	3	0	0	0
	9	5	1	3	2	1	1?	2	0	0	0
	16	6	2	3	3	1	0	3	0	0	0
	19	6	2	3	3	–	0	2	0	0	–
	20	–	0	1	–	–	–	3	0	–	–
C	6	5	4	0	3	1	0	0	2	0	0
	14	6	5	0	3	1	0	0	2	0	0
	15	6	5	0	3	1	0	0	2	0	0
D	8	4	4	3	0	1	0	0	0	2	0
	12	6	5	3	0	1	0	0	0	2	0
	17	4	3	3	0	1	1	1	0	2	0
E	1	5	4	3	3	0	0	0	0	0	0

tion, since not all hand pollinations are successful even when the plants are known positively to be fertile. Some of the exceptions, where seed is obtained from pollinations within one class, are undoubtedly due to end-season pseudo-fertility. Sixteen of the plants can be classified without any inconsistency, and the results as a whole show the existence of different classes. While the number of plants

tested is necessarily small, on account of the labor involved in making so many hand pollinations, it is clearly indicated that the numbers of plants which fall into the several classes are not equal. Some classes contain a large number of plants and some only a few.

The interpretation that East and Park give to account for these results is as follows: They assume that *N. Forgetiana* is heterozygous for several factors which determine the behavior of the plants with respect to seed formation, and that the homologous chromosomes of *N. alata* are heterozygous for different multiple allelomorphs of the same factors. For the purpose of giving a concrete demonstration of the way this system works, they have assumed that three such factors were involved in making the original cross. The two plants are represented diagrammatically as follows:

N. Forgetiana		*N. alata*	
A	A′	A″	A‴
B	B′	B″	B‴
C	C′	C″	C‴

The hypothesis is put forward that fertilization fails to take place whenever exactly similar combinations of these factors are brought together, but two plants need differ by only one of these factors in order to be fertile when intercrossed. The gametes of any one plant all function alike according to the factorial composition of the individual that produces them and not according to the factors they carry. For that reason, every plant is sterile with its own pollen and is either completely sterile or completely fertile with other plants. There is no selective action among the gametes such that part of them can function and part can not. Fertilization is determined apparently by the cytoplasmic envelope in which the nucleus is carried as a passive body, not to be active until after fertilization.

These plants of the two pure species which were used for crossing have the composition AA′ BB′ CC′ or

A″A‴ B″B‴ C″C‴, and by hypothesis neither plant can be fertilized by gametes borne on a plant of like constitution. These plants of *N. Forgetiana* and *N. alata* form 8 types of gametes. *N. Forgetiana*, for example, produces gametes of the composition ABC, A′B′C′, A′BC, AB′C′, ABC′, A′B′C, AB′C, A′BC′. The other species forms its gametes in the same way. The progeny will therefore be composed of $8^2 = 64$ groups of individuals which are sterile within the group, but fertile when cross-pollination takes place between different groups. If there is linkage, the groups will vary in the number of individuals which they contain, but it is not necessary to consider this complicating feature here: Since neither parental combination, AA′ BB′ CC′ or A″A‴ B″B‴ C″C‴, is produced in the first generation, after crossing the two species, all classes in that generation will be fertile when back-crossed to either parent.

Reduction in number of inter-sterile classes by inbreeding.—In later generations it is possible, by recombination, for some of these factor pairs to become homozygous. For example, two plants with the composition AA′ BB′ CC and A″A‴ B″B‴ CC will each form only 4 different kinds of gametes. The factor C, being homozygous, can be left out of consideration. The first plant forms gametes AB, A′B′, AB′, and A′B. In the same way the other plant forms gametes A″B″, A‴B‴, A″B‴, and A‴B″. With the factor C eliminated in this case, the progeny will fall into 16 classes instead of 64 as with three factor differences. In this way simplification can go on, and this is promoted by inbreeding. Finally AA′ may be crossed with AA″. Four classes will be formed: AA, AA′, AA″, and A′A″. When AA is mated with AA′ only two intra-sterile, inter-fertile classes will be formed. The simplification can go no further than this, because no plants which are exactly alike in all factors can be paired and produce seed normally.

Crosses of self-sterile with self-fertile plants.—These self-sterile plants of tobacco and other species which show

the same type of sterility, when crossed with self-fertile plants of the same species, give progeny all of which produce seed with their own pollen. When self-fertilized or bred together, they give in the second generation self-fertile and self-sterile plants, following the familiar rule of a monohybrid. In other words, self-sterility is a recessive condition, and in the species of tobacco studied by East and Park there seems to be only one factor involved in the difference between self-fertility and self-sterility. In other plants, the situation may be found to be more complicated than this. We can think of one factor *F* which, when present in the dominant condition, renders the system of sterility factors just described entirely inoperative. With the recessive factor *f* in the homozygous condition, the system works as outlined. In this way self-sterile and self-fertile plants of exactly the same appearance may exist side by side in the same variety.

With this theoretical interpretation, if we employ different numbers of factors as the number of inter-sterile classes demand, most of the facts of self-incompatibility in tobacco and many other plants fall into line. It should be remembered that this is merely a tentative interpretation, and it can hardly be hoped that this comparatively simple explanation will suffice to account for all the manifestations of sterility of this kind in all plants. It is the beginning of a definite analysis and has already made possible conclusions of practical importance, as will be shown later.

Pollen-tube growth in incompatible pollinations.—The floral parts of self-incompatible plants are typically normal and produce abundant pollen, which germinates on the stigmas but is unable to grow fast enough to reach the ovary before the pistil withers and falls off. Something inhibits the normal rate of pollen-tube growth. Compatible pollen tubes are stimulated to a more rapid growth and reach the ovary in time for fertilization to take place. In cases of end-season pseudo-fertility, the incompatible pollen tubes for some reason are able to grow faster than

normally and reach the ovary before the flowers drop off. Fertilization in these cases takes place normally, showing that there is no abnormality in the fertilizing mechanism itself.

Incompatibility in animals.—Only one clear case of incompatibility is known to exist in animals, and this is in one of the lower forms. As far as known, none of the domestic animals exhibit this phenomenon, although there are certain matings which are never fertile even though both members are able to produce young when bred with other individuals. It is possible that something corresponding to incompatibility in plants may exist among the higher animals and has not yet been recognized. The fact that these animals are bisexual prevents its showing up in large numbers, and the comparatively few cases of cross-sterility might easily escape identification.

Disadvantage of incompatibility in cultivated plants.—Although self-incompatibility is widespread in plants, it is essentially a special function, apparently serving the same purpose as floral devices, differences in time of flowering, and other numerous means of promoting cross-fertilization and consequent germinal mixing. However useful self-incompatibility may be in nature, it is distinctly disadvantageous in economic plants and causes considerable loss annually, particularly in fruit growing. Space must be used in orchards to grow inferior varieties to supply the need of suitable pollen. In Oregon, according to Gardner, three varieties of sweet cherries which are the most valuable commercially—Napoleon, Lambert, and Bing—are all self-sterile and also cross-sterile with each other. They must be interplanted with other varieties in order to give satisfactory results.

The history of sweet cherry growing in the West is typical of horticultural development in new regions. At first a large number of varieties are grown in order to find the most suitable. In these mixed plantings, the chances are good that all varieties will be well fertilized with com-

patible pollen. A few varieties are then chosen for their productiveness and other fruiting qualities, and planted in large orchards. Often only one or at most a few varieties are used. When they come into bearing several years later, it is found that these varieties may be both self-sterile and inter-sterile, with the result that they are not nearly as productive in the large orchards as they are in the trial plantings. Provision must then be made for proper pollination, with loss of considerable time in which the orchard should have been bearing profitably.

Eliminating incompatibility.—Future breeding operations should aim to remove this type of sterility as far as possible, although this will be difficult and possibly not worth while in every case. From the work of East and Park, it is clear that it is impossible to eliminate sterility due to incompatibility when starting with plants that are all self-sterile. No amount of selection can increase the chances for fertile matings, and close inbreeding will certainly decrease them, bringing about a condition in which the plants are not only self-sterile but cross-sterile in many combinations. Unless there are some self-fertile plants in the original material, it is necessary to cross with self-fertile individuals, and in either case it is necessary to have at least one self-fertile plant in every cross-mating in each generation in order to make it possible to get full fertility in the end.

Selective fertilization.—On account of the frequent occurrence of self-sterility among plants, it has been generally held that even plants which are self-fertile are more easily fertilized by pollen from other plants of somewhat different composition. Since plants are so notably stimulated to greater development after crossing, the prepotency of foreign pollen seemed quite plausible and was taken as an adaptation favoring cross-fertilization when different kinds of pollen were brought to the flowers at the same time. The same argument has been applied to animals, and it has even been assumed that cross-fertilization at some time is

equal-sized plants, similar shape of seeds and ears, and the same time of ripening, and differing only in color of endosperm and other minor details, are tested against each other, by the method of mixed pollination, the percent increase in weight of crossed seeds over self-fertilized seeds is comparatively small. The selective action is also small, but significant and in favor of self-fertilization. On the other hand, when two types of corn which differ markedly in size, time of growth, form and structure of all parts of plant, as well as in the texture and color of the endosperm, are paired together, the greater difference in germinal constitution is shown by the large increase in weight of crossed seeds. In this case the selective action is also pronounced, resulting in almost complete self-fertilization in both plants when the same choice of two kinds of pollen is offered to each.

The tendency towards sterility.—There is thus exhibited a tendency which operates to set organisms apart. Although it tells us nothing as to how these differences which bring about the selective action arise, it indicates that the impossibility of uniting radically different forms of life is due to the accumulation of germinal differences until a point is reached where sexual fusion can not take place at all. From a survey of a large number of crosses between different species in the genus *Nicotiana*, East found: (*a*) crosses that produce viable offspring; (*b*) crosses that produce seed with embryo, but go no further than the resting stage of the seed; (*c*) crosses that produce seed containing no proper embryo; and (*d*) plants so different that no seed of any kind is formed when crossed. Actual fusion may take place between gametes which are so different in character that the zygote can not develop, or between gametes in which the male cell does not bring in the proper substance to stimulate development. In the last analysis the inability to cross-fertilize is taken as marking specific differences, even where visible differences are lacking. Incompatibility, therefore, results when the germinal differences are too great, as it also results in special instances when organisms are alike

with respect to certain factors. The two types of incompatibility are fundamentally quite distinct and probably have nothing in common.

Assortative mating.—The selective action in plants has a close parallel in animals in the assortative mating which favors the pairing of like with like. This is shown by many forms from the lowest to the highest. A living organism, like a machine, works better when all the parts are harmoniously adapted to each other, and this can only be brought about by long association and elimination of inharmonious elements. Cross-fertilization between different forms may bring about a more favorable combination of hereditary factors, which gives the resulting offspring a temporary advantage and may more than offset any lack of balance in the interacting germplasms. But all the evidence indicates that homozygosity, rather than heterozygosity, is more favorable to growth and reproduction, as long as the best heredity is present in both cases.

Sterility due to impotence.—This brings us to the second type of inherited sterility, which is due to derangement of those parts of the organism which are concerned with reproduction. If the condition is such that the organism is unable to reproduce under any circumstances, this type of sterility is called **impotence** and is quite distinct from **incompatibility.** In the latter case, as we have just seen, there is no structural derangement, and the sex organs and germ cells are entirely normal except that particular combinations of certain individuals simply do not function while other combinations of the same individuals do.

Limits of hybridization.—The limits beyond which hybridization is not possible differ widely in various families. Many apparently good species, which are uniform among themselves and quite different in external features, will cross readily and their progeny are fully fertile. Even different genera and different families have been brought together, showing that the method of classification used by the systematists is more or less arbitrary. On the other

hand, some forms which are very much alike in appearance can not be intercrossed.

Manifestations of impotence.—In most crosses between different species and different genera, there is a noticeable effect upon the organs of reproduction even when there are no other unfavorable results. The manifestations of sterility resulting from crossing are so diverse that it is not possible to describe them fully; but a general series can be arranged, as follows, according to the degree of similarity of the forms united:

1. When the individuals are exactly alike in their germinal constitution, there is no change in size or feature. Crossing is entirely without effect and gives exactly the same results as self-fertilization, whether the plants are homozygous or heterozygous.

2. Minor differences in constitution result in an alteration of appearance but have no noticeable heterotic effect upon size or ability to reproduce. This is the usual result of crossing different strains belonging to the same variety.

3. Greater differences in hereditary make-up bring about an increased size of the hybrid offspring above the average of the parental races. This is the familiar hybrid vigor so commonly displayed to a greater or less extent in variety crosses in plants, and in crossbred animals and in related species hybrids. Fecundity and fertility are usually not changed, but the larger growth and greater vigor make possible a greater productiveness. *Nicotiana alata* and *Nicotiana Langsdorffii*, for example, are distinct species showing differences in nearly all characters, and their hybrid grows normally and is completely fertile. The skunk (*Mustela putorius*) and the ferret (*Martes furo*) belong to different genera. but they can be crossed and give normal fertile young.

4. Still wider germinal differences may result in offspring having the same or greater vigor than the parents but the hybrids exhibit reduced fertility or even total sterility. This is the result to be expected from most species hybrids.

The increase in growth is sometimes extreme. The radish (*Raphanus sativus*) and the cabbage (*Brassica oleracea*) belong to different genera but can be hybridized, as has been done on at least two different occasions. Both times the crossed plants grew enormously. (See Fig. 162.) This

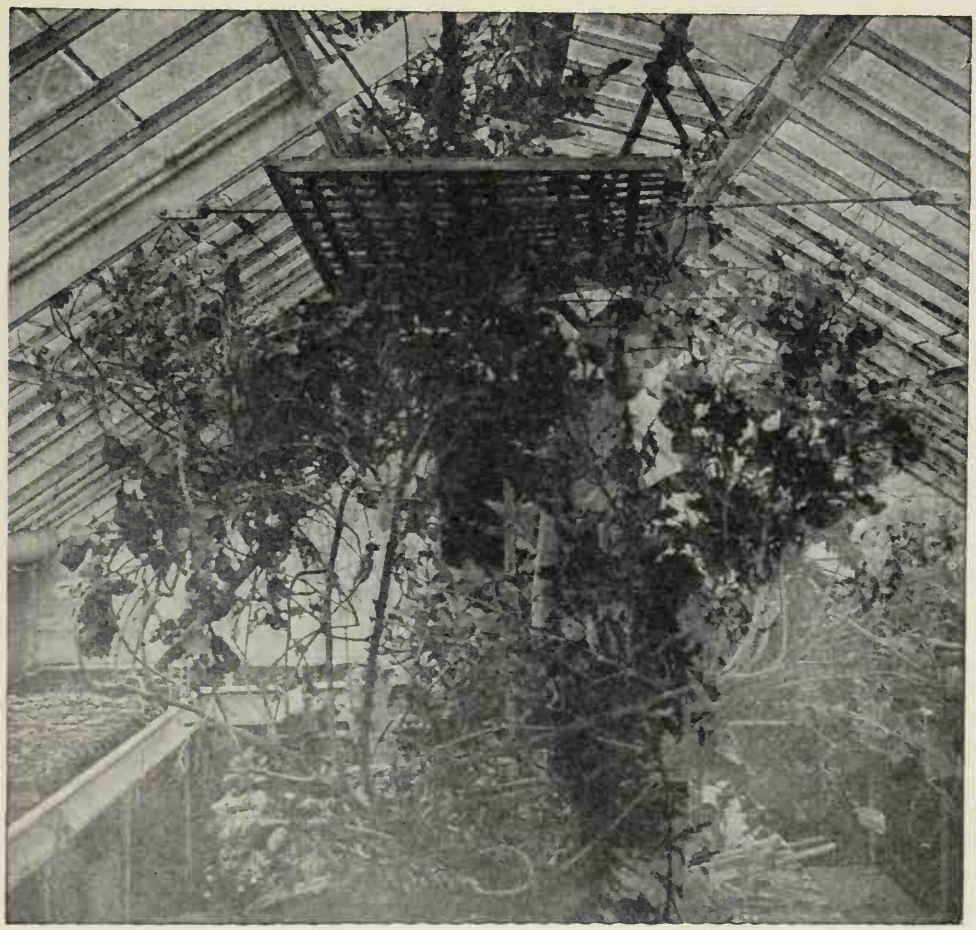


FIG. 162.—Sterile hybrid produced by crossing the radish, *Raphanus sativus*, with the cabbage, *Brassica oleracea*. (After Gravatt in the Jour. Heredity.)

rampant hybrid flowered but produced no viable seed. Some wide crosses give no seed when self-fertilized but can be back-crossed to one or the other parent. This is the case with the hybrid between rye and wheat, which can be crossed back with either parent but rarely sets seed by selfing as the pollen is almost entirely aborted. On the other

hand, the cross of *Antirrhinum majus*, the common snapdragon, with another species *A. siculum*, made by Baur in Germany, gave a hybrid plant with entirely sterile ovules but some fertile pollen grains. Many animal crosses are sterile in the male and fertile in the female. This result was obtained by Detlefsen in hybrids between different species of guinea pigs. The domestic cow (*Bos taurus*) gives the same result when crossed with the American buffalo (*Bison americanus*), with the yak (*Bibos gruniens*),

FIG. 163.—Sterile hybrid produced by crossing the ass with the zebra. (After Riley in Proceedings of the American Breeders' Association.)

with the gayal (*Bibos frontalis*), and with the gaur (*Bibos gaurus*). The mule hybrid, resulting from the mare bred to a jack, is strong and sturdy but sterile in both sexes. The reciprocal combination, the hinny, is similar in appearance and likewise sterile. The zebra-horse and zebra-ass hybrids are also sterile.

5. Other species hybrids, which can usually be made only with difficulty, may exhibit a reduced size and lessened vigor together with complete sterility. These manifesta-

tions are brought out in all possible degrees. Some tobacco hybrids, made by East and Hayes, produced seed which would not germinate after careful testing even though endosperm and embryo tissues were formed. *Nicotiana tabacum* crossed with *N. paniculata* and *N. rustica* with *N. alata*, as shown by East, gave seed which sprouted, but the plants were weak and died before flowering. In some other tobacco crosses, the plants develop slowly and in the end are smaller than either of the parents. The hybrid between the sheep and the goat can be made, but apparently with some difficulty, and it is not particularly vigorous. A close approach to the extreme limit of hybridization is well illustrated by a cross of two species of barley, made by Malloch. The two species differed greatly in all parts of the plant. Two hybrid seeds were produced and germinated, but both seedlings were very abnormal and consisted of but a single leaf which did not attain a greater height than a few inches, and the plants soon died. Two species of the tar weed (*Crepis capillaris*) and (*C. tectorum*), when crossed, behaved in much the same way as the barley crosses, as described by Babcock and Collins.

6. Finally the point is reached where crossing is impossible. No seeds are produced by the application of pollen when the differences in germinal constitution are too great. No one has succeeded in crossing wheat with oats, or either with barley. Apples and pears can not be crossed, although the differences between them seem to be no greater than between apricots and plums and between plums and cherries, some varieties of which can be crossed. Similarly, animal sperm is wholly ineffective when the forms united are too diverse. Sometimes hybrids can be made one way and not the other. The cross of cabbage by radish is apparently unsuccessful, although the reciprocal cross, as just noted, can be made. In both animals and plants, differences in the structure of the sex organs may sometimes prevent the gametes from being brought together. Even when these difficulties are overcome by artificial means, as

they sometimes can be, fusion of the germ cells may be impossible.

Effect of maladjustment on gamete formation.—Sexual reproduction is particularly dependent upon the harmonious interaction of all the elements that go to make up the body. An unbalancing or lack of proper adjustment may not seriously interfere with the ordinary developmental process, and in fact the union of somewhat different germinal complexes may even result in a larger growth; but when the time comes for the formation of germ cells in preparation for reproduction, it is then that the diverse elements brought together by hybridization are unable to function properly. In the mule hybrid, division of the body cells takes place normally, but at the reduction division the chromosomes break down and degenerate. In this case all the germ cells behave in this way and the animals are completely sterile. In other cases a part of the germ cells may be able to function. It is a common feature of many plant hybrids to have some aborted pollen grains.

Selective elimination of gametes.—As a result of partial sterility of this kind, certain classes of gametes fail to develop while others are able to survive. The elimination is selective and, in general, the ones that survive contain a major portion of the chromosomes of one or the other parent. The aborted gametes contain part of one and part of the other and are unable to develop because of the lack of adjustment between the diverse elements. This selective elimination of gametes is shown in several species hybrids, whose self-fertilized progenies have been grown and found to give some offspring which are an exact return to one or the other parental type. In these crosses great differences separate the parental species, and with random assortment of the gametes and fertility of all combinations the recovery of the parental types would not be expected except as a very rare occurrence in enormous numbers of individuals. The fact that the parental types have been obtained in appreciable numbers is practically proof that many mixed

gametes are not viable or the embryos resulting from them are unable to develop.

Wheat-rye hybrid.—The elimination of certain combinations is well shown in hybrids between wheat and rye. This cross has been made or reported as occurring naturally by some twelve different investigators. It is a good illustration of a cross which is difficult to make, as only a few seeds are produced in many attempted pollinations. Jesenko obtained only six seeds as the result of one thousand applications of rye pollen on wheat stigmas. The reverse cross could not be made at all in many trials. He found that all the hybrid plants failed to have viable pollen, as shown by cytological examinations and testing on wheat stigmas. When pollinated by wheat the hybrids produced three seeds in about one thousand stigmas pollinated. With rye pollen, only one seed was secured in 4800 attempts.

Gaines has recently reported partially fertile hybrids between various varieties of wheat with Rosen rye, made in large numbers and either way pollinations were made.

Reversion of partially sterile hybrids to the parental types.—The resulting back-crossed plants were strikingly similar to each parent with which they were pollinated. When the hybrid was pollinated by wheat, some of the resulting plants were exactly like the wheat parent and the others showed only slight indications of rye characters. The reciprocal back-crosses gave similar results in that the plants were wholly or almost entirely rye in appearance. It is a plausible explanation to assume that those ovules which contain all wheat or largely wheat chromosomes can be fertilized by wheat pollen, and in the same way only the predominatingly rye ovules can be fertilized by rye pollen and give viable embryos. For this reason it is to be expected that wide crosses will tend to revert to either parent.

Elimination in tobacco hybrids.—Similar results have been obtained by East and by Goodspeed and Clausen with tobacco. A hybrid, described in detail by the latter investigators, between the cultivated *Nicotiana tabacum* and the

wild *N. sylvestris*, is particularly illuminating. The first-generation plants are almost completely sterile; when they are grown under reduced conditions of culture, however, they will set some seed with pollen of either parent but never produce more than about 1 percent of the number of seeds which the parents do normally. The resulting back-crossed plants are variable in type, but about 10 percent closely approximate the parent which supplied the pollen and others reduplicate the first-generation hybrid plants.

Interpretation of partial sterility.—Since tobacco has 24 pairs of chromosomes and the two parental species presumably differ in all of them, there would be produced normally an enormous number of different combinations in the gametes even if no crossing-over took place. Only one gamete in 16,777,316 on the average would have the entire chromosome set of either parent. The practically complete return to either parent can only be accounted for by the assumption that only those gametes of the hybrid which carry exactly or nearly the complete chromosome set of one or the other parent can produce living embryos when united with gametes of either parent. Assuming that a gamete with more than 5 of one set and less than 19 chromosomes of the other can not form a harmonious combination with the chromosome system of either pure race, Goodspeed and Clausen have set down the theoretical result to be expected, as shown in Table XXXVIII.

According to their interpretation, which is an amplification of a theory first proposed by East, two classes of viable embryos can be formed. Those gametes which are mainly similar in composition to the pollen applied produce plants closely resembling that species, while those gametes which are mainly of the opposite set unite with the same generative nuclei to produce plants like the first-generation hybrid. Similar results follow when the hybrid plants are back-crossed with the other parent. Gametes which are intermediate in composition are unbalanced and are unable to function properly in combination with the chromosome

TABLE XXXVIII

CHROMOSOME COMBINATIONS IN THE GAMETES OF THE F_1 HYBRID OF *N. Tabacum* BY *N. Sylvestris* AND THEIR THEORETICAL BEHAVIOR WHEN BACKCROSSED WITH EACH PARENT

Data from Babcock and Clausen

Condition of Gametes	*Ratio of N. Tabacum* to *N. Sylvestris* Chromosomes	Proportionate Number of Gametes	Progeny When Pollinated with *N. Tabacum*	Progeny When Pollinated with *N. Sylvestris*
Functional.	24 : 0	1	Plants resembling the *N. tabacum* parent and of various degrees of fertility.	Plants resembling the F_1 and abnormal plants but all nearly completely sterile.
	23 : 1	24		
	22 : 2	276		
	21 : 3	2024		
	20 : 4	10626		
	19 : 5	42504		
Non-functional	18 : 6	134596	No viable seeds.	No viable seeds.
	17 : 7	346504		
	16 : 8	736321		
	15 : 9	1307504		
	14 : 10	1961256		
	13 : 11	2496144		
	12 : 12	2705456		
	11 : 13	2496144		
	10 : 14	1961256		
	9 : 15	1307504		
	8 : 16	736321		
	7 : 17	346504		
	6 : 18	134596		
Functional.	5 : 19	42504	Plants resembling the F_1 hybrid and nearly completely sterile.	Abnormal, infertile plants and fertile plants closely resembling *N. sylvestris*.
	4 : 20	10626		
	3 : 21	2024		
	2 : 22	276		
	1 : 23	24		
	0 : 24	1		

set of either parental species. Using the arbitrary number of 5 chromosomes as limiting the amount of unbalancing permissible, they calculate that only 0.7 percent of the gametes will be functional. This agrees closely with the actual number of seeds formed.

As many investigators point out, it is easier to recover the parental type in such a partially sterile species cross than in ordinary variety crosses. Cultivated varieties of tobacco, when crossed, give such an enormous number of

FIG. 164.—A partially sterile hybrid between wheat and rye. (After Love in Jour. Heredity.)

different variations that it is practically impossible to recover exactly either parent that entered into the cross. This indicates that in wide, partially sterile crosses there is an elimination of both gametes and embryos.

Fertility resulting from a partially sterile hybrid.—Love and Craig, at the New York Station, have obtained a fertile plant from the cross of wheat and rye without back-crossing. The first hybrid plant had all the characteristics of a wheat-rye hybrid and was almost sterile, but did produce one seed when self-pollinated, contrary to the results obtained by Jesenko. This seed gave a plant very similar to its F_1 parent, and for that reason it was considered not

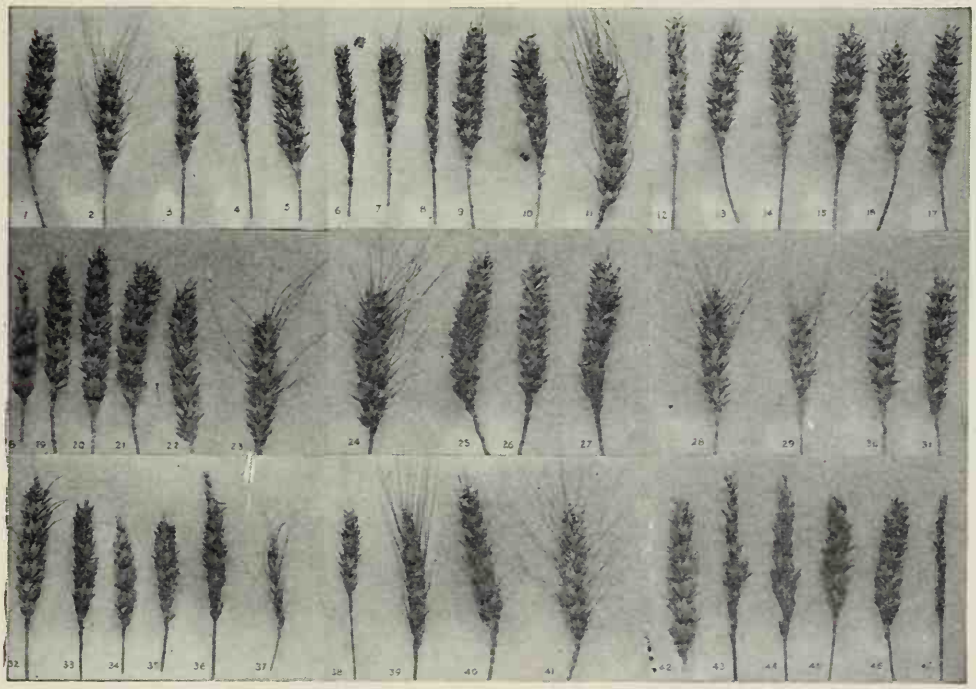


FIG. 165.—Heads from different plants of the F_4 generation from the partially sterile hybrid between wheat and rye. (After Love in Jour. Heredity.)

to have been an accidental back-cross with either wheat or rye. The second-generation plant again formed only one seed. The third-generation plant produced a large number of seeds, and the resulting plants gave a wide range of types (Fig. 165). These were, in general, more like wheat than rye and showed marked differences in fertility. They did, however, show many of the qualities of rye, and the character which is being chiefly followed is the well-known winter hardiness of rye. If it is possible to recombine cold resist-

ance of rye with a satisfactory quality of wheat, such a plant should have great value.

The possibility of producing radically new forms from recombinations in partially sterile hybrids, indicated in the wheat-rye hybrid of Love and Craig, is well brought out in a cross of *Nicotiana rustica humilis* and *N. paniculata,* made by East. Both parental species are very uniform but differ in practically every feature. The first-generation

FIG. 166.—Representative seeds from some of the heads shown in Fig. 165. Several plants produced no seeds, while in some others the seeds were shrunken and abortive. (After Love in Jour. Heredity.)

plants were no more diverse than either parent and exhibited features of both. The parental races were fully fertile, but the hybrid plants produced only from 3 to 4 percent of the normal amount of seed for both parents. The second generation, grown from seed of self-fertilized plants, was astonishingly variable in height, spread, size and shape of leaves, texture, and color of all parts. In some 300 plants grown, practically every individual could be classed as a different variety. A few of the plants were an exact return

to one or the other parent. Some plants reproduced very closely other varieties of *N. rustica*, which differ quite noticeably from the variety *humilis* used in making the cross.

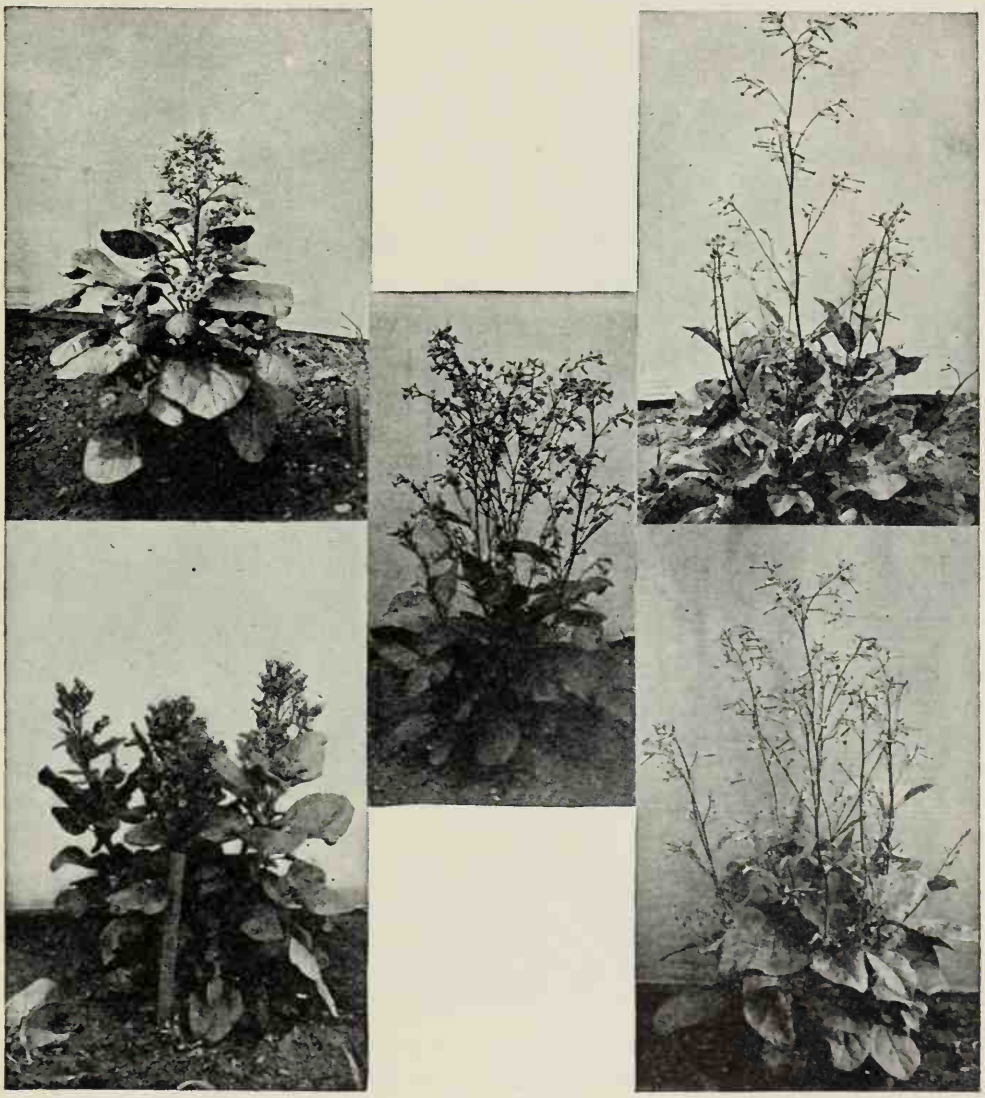


FIG. 167.—A partially sterile hybrid in tobacco, *Nicotiana rustica humilis*, upper left; *N. paniculata*, upper right; the F_1 in the center; and two F_2 plants which reduplicated the original types below. (After East in Genetics.)

The two parents and the first-generation hybrid, together with the extracted types which reduplicate the parents, are shown in Fig. 167. In Fig. 168 are shown the extreme second-generation types. The diversity in flower form and

size and shape of leaf are demonstrated in Figs. 169 and 170. Variability in development in nearly all characters went beyond the limits of both parental races in both directions. The second-generation plants, as a whole, were more like the *rustica* than the *paniculata* parent.

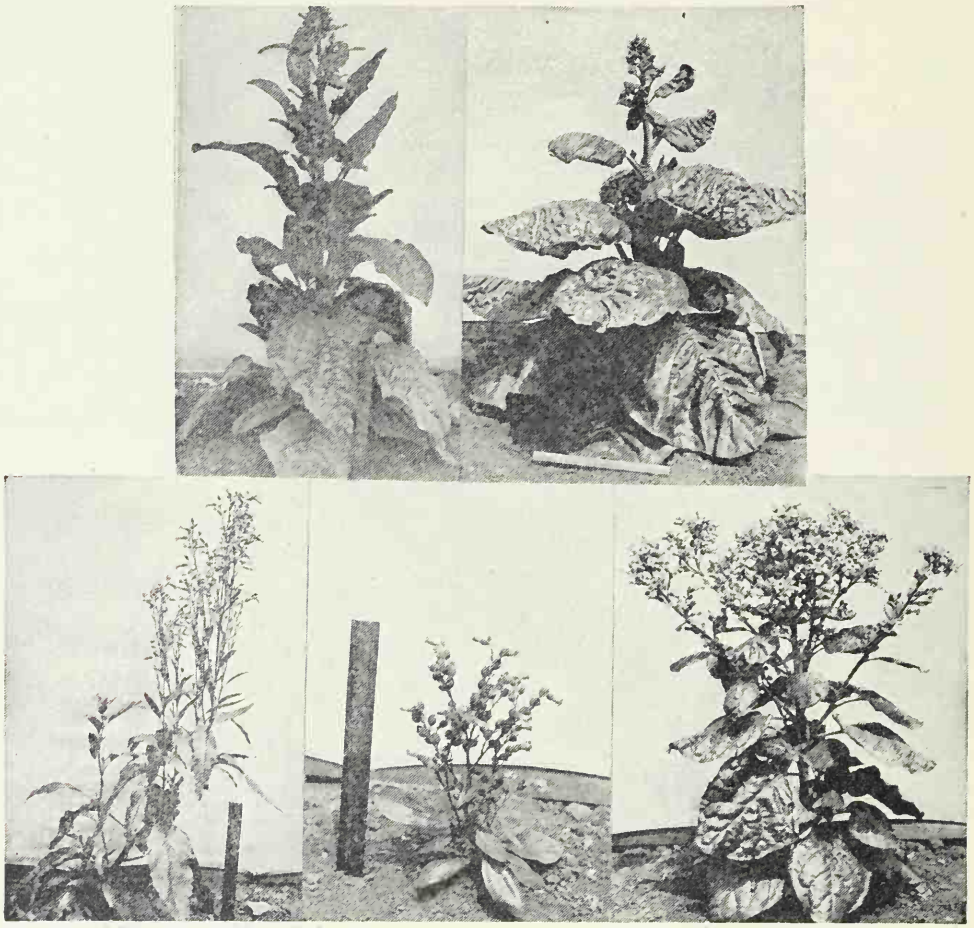


FIG. 168.—F_2 plants from the cross of *N. rustica humilis* by *N. paniculata*, showing extreme diversity in size and form. (After East in Genetics.)

Uniformity of segregates from partially sterile hybrids.—All degrees of fertility were exhibited in this generation, ranging from almost total sterility of the first crossed plants up to the full fertility of the parents. When succeeding generations were grown, these diverse plants showed an unexpected uniformity in their progenies. They bred true, from the start, to their individual type. Although they

were somewhat reduced in variability in later generations, they must have been nearly homozygous in the second generation. Fertility in general improved in the later generations, and in most cases an abundance of viable seed was produced.

How partially sterile hybrids differ from variety crosses.—This partially sterile species hybrid differs from the usual and expected results from variety crosses in two outstanding features. First, the recovery of the grandparental types in

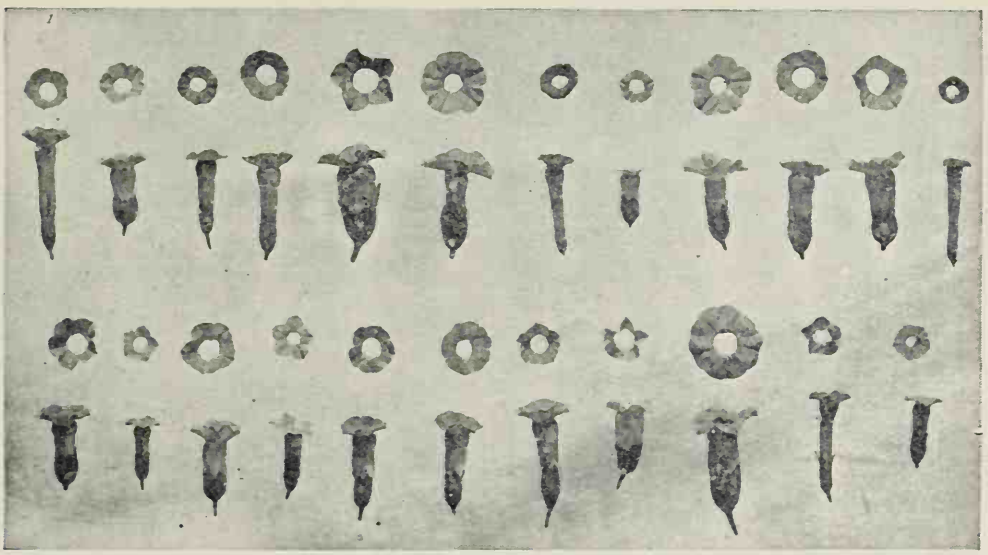


FIG. 169.—Flowers from the parental species and twenty-one plants of the F_2 generation of *N. rustica humilis* by *N. paniculata*. Upper right, *N. paniculata;* lower *left, N. rustica humilis.* (After East in Genetics.)

such a small number of F_2 individuals shows that not all the possible recombinations are realized. Second, the F_2 individuals, as shown by their F_3 progenies, are much more homozygous than similar plants from fully fertile crosses.

Value of partially sterile hybrids in breeding.—The importance of these results from partially sterile species hybrids, for practical plant and animal improvement, can hardly be over-estimated. Crossing between any unlike forms brings about variability; but when there is normal fertility, the intergrading forms are so numerous, and the

differences between them are so small, that it is difficult to find those individuals which may be a betterment over

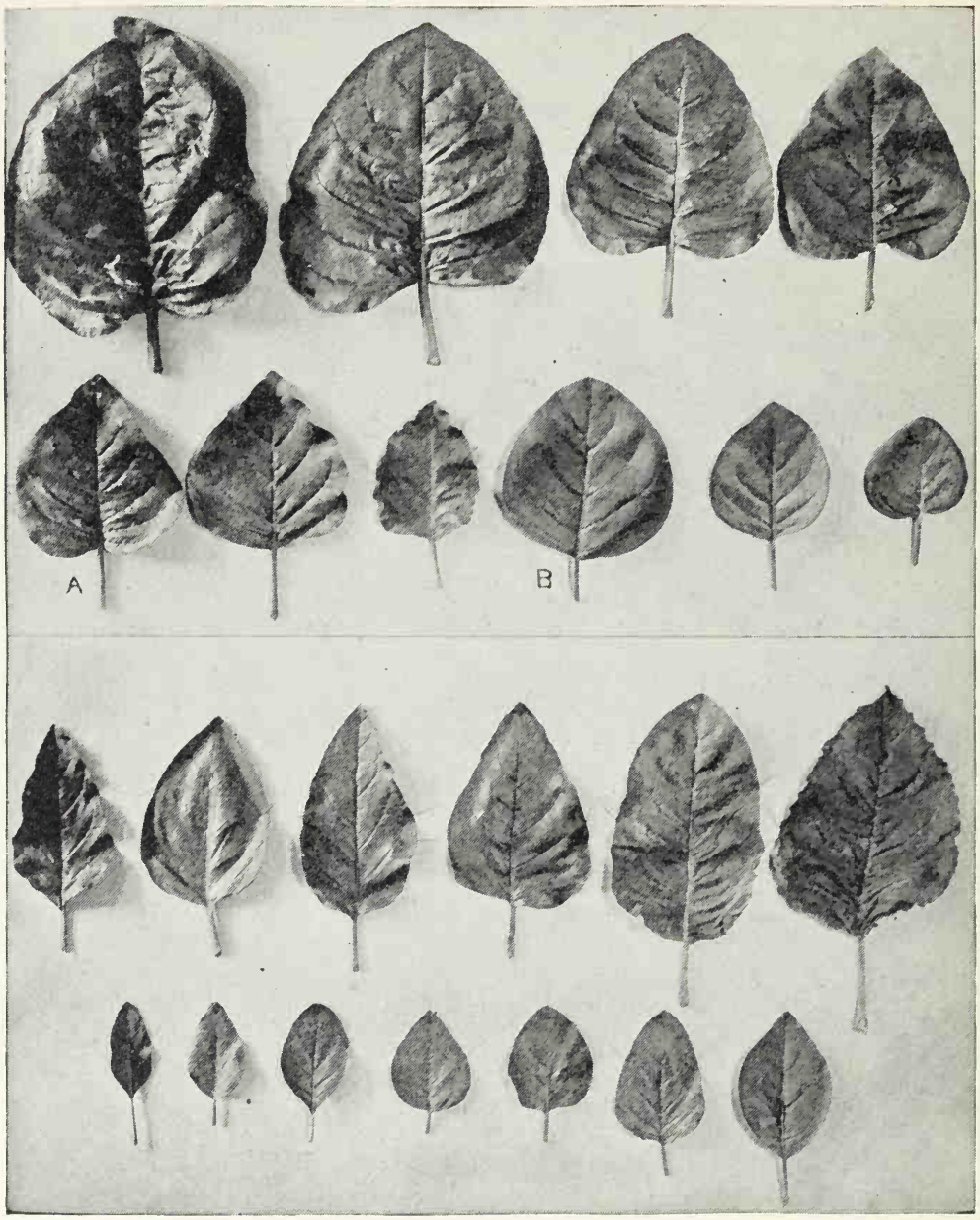


FIG. 170.—The largest leaf on each of the twenty-one plants of the F_2 generation of the cross of *N. rustica humilis* by *N. paniculata* of which flowers are shown in Fig. 169. *A* and *B* are from the two parental species. (After East in Genetics.)

existing forms. Furthermore, there are not such great possibilities of radical improvement. The great majority

of the offspring from closely related crosses are heterozygous in many factors, and must be fixed by many generations of selection.

On the other hand, when the crosses made are so wide that almost complete sterility results, the incompatibility of many chromosome combinations leaves only a small residue which is able to function. Apparently the unfavorable combinations perish, and only the compatible combinations survive. These are extremely diverse in form. The greater the differences in the species that are crossed, the greater is the opportunity for entirely new variations. Among these there may be a few that are really valuable. Experimental evidence thus shows that the greatest opportunity for originating radically new and valuable kinds of animals and plants lies in the crossing of races which are as different as it is possible for them to be without failing to give some degree of fertility in their offspring.

As brought out in Chapter X, there is considerable evidence to show that those families and genera, which under natural conditions have varied the most widely, and still retained sufficient compatibility to allow extreme forms to be crossed and give more or less fertile progeny, are the ones that have given the most valuable animals and plants. The genetic, as well as the historical evidence, points to a mixed origin for most of our important domesticated forms. Great possibilities lie in the many new species which are constantly being introduced.

Sterility due to chromosome irregularities.—Sterility frequently results from chromosome aberrations. As brought out in Chapter VI, Bridges has shown that the two X chromosomes in the normal female of Drosophila may not always separate at the reduction division, but both may go into one daughter cell, leaving the other without a representative of this particular chromosome. When a defective gamete of this kind pairs with a normally female-producing gamete from the male, the result is an individual which is lacking in one member of the four chromosome

pairs. Such individuals are normal in appearance but are completely sterile. Other chromosome anomalies are formed by non-disjunction in this way, but the embryos die soon after fertilization.

Lethal factors.—In the complicated chain of chemical reactions that take place in the development of an organism from the fertilized egg to the adult, many things may go wrong. Muller has shown that the most frequent mutations in Drosophila are those lethal factors which cause the death of the embryos soon after fertilization whenever segregation brings the same factor together in double dose in one individual. Many other factor changes do not kill the organism but seriously retard its growth and result in abnormalities in various parts. Since the process of reproduction sums up the energies of the entire organism and in many ways is the most difficult task it has to perform, it is to be expected that many of the variations which occur would result in partial or complete derangement of the sex organs and germ cells and cause partial or complete sterility. Such forms of inherited sterility are common and can be grouped according to the stage of the reproductive process in which they operate.

Aborted pollen.—Many plants show varying proportions of aborted pollen grains. This is due in part to the condition of the plant with respect to nutrition and other environmental factors. There are also hereditary factors which cause a destruction of certain gametes, irrespective of the condition of the plant. Belling has shown that, in the velvet bean, certain individuals may have half of their pollen grains regularly empty and half of the ovules with embryo sacks aborted. This condition he calls semi-sterility. These plants were found in the progeny of a cross of two entirely fertile races of velvet beans. Half of the progeny of the semi-sterile plants show no destruction of the gametes and remain normal in subsequent generations, while the other half again regularly abort half of their germ cells.

Abortion in pollen tetrads.—In Rhododendron, a plant in which the pollen grains adhere in tetrads, each group of four cells is the product of two successive divisions of a pollen mother cell. One of these divisions is the reduction division, so that in a hybrid plant the two cells which make up one pair of a tetrad are alike. Belling has found certain plants of this species with half of their pollen grains aborted, and in every case two of the cells of each tetrad are empty.

Sterility in relation to chromosome pairing.—Blakeslee and Belling have obtained Jimson weeds with an odd number of chromosomes, due to some inequality in the reduction division. Such plants produce gametes half of which have an even number and half an odd number of chromosomes. The gametes with the odd number of chromosomes regularly abort, giving a result which is the same as in the above case of semi-sterility in the velvet bean. Chromosome aberrations of this kind are now believed to be an important cause of partial sterility, which may persist in many plants and animals. Wodsedalek has found that the horse and ass differ in the number of chromosomes, in such a way that the mule results from the union of an egg cell containing 19 chromosomes with a sperm containing either 32 or 33. The germ cells of the mule regularly degenerate at the reduction division, apparently because of the abnormal chromosome distribution. From the results obtained with plants, it is to be expected that mules might occasionally produce functional germ cells, and there seem to be a few authentic cases in which offspring have been obtained.

Destruction of embryos.—More generally, lethal factors do not act upon the gametes directly but result in the destruction of the embryo soon after fertilization. A case has long been known in mice in which a recessive Mendelian factor is responsible for the regular production of progenies which are on the average one-fourth smaller in number than those of other mice under the same conditions. Such mice also have a characteristic yellow coat color. Whether

this color is part of the effect of this lethal factor or is completely linked with such a factor is not known. It has been

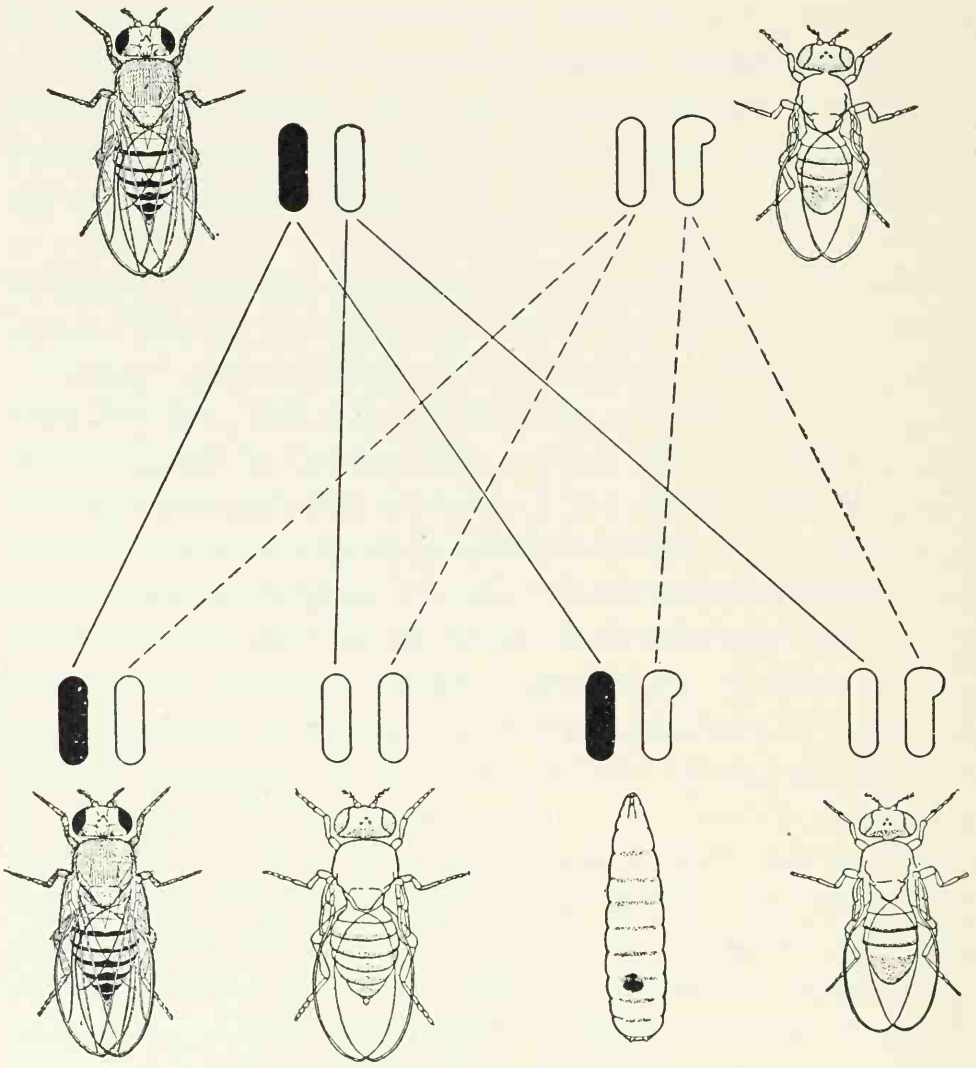


FIG. 171.—Diagram showing the inheritance of a sex-linked recessive lethal factor in Drosophila. The sex chromosome carrying the lethal factor is represented by the black rod. Half of the males in the progeny die in the larval stage from a tumor-like growth controlled by the recessive factor. In this mating the normal male parent has the recessive eosin eye color, so that the normal red-eyed females in the progeny alone carry the abnormality. (After Morgan in Middleton Goldsmith Lecture.)

established beyond doubt that these yellow mice are heterozygous for a vital factor which in the homozygous recessive condition stops the growth of the young mice. The aborted

embryos have been found in the expected numbers when the mice were examined shortly after pregnancy.

Similar cases are known in other rodents and in Drosophila. It is evident that such completely lethal factors must be recessive, or otherwise they would be immediately eliminated. Usually they have some visible effect in the heterozygous condition, as in the yellow mouse, but this is merely an intermediate stage between the normal dominant and abnormal recessive conditions. The homozygous, true-breeding recessive can not be obtained. Such factors are sometimes classed as dominants on account of the change which they bring about in the heterozygous condition, but in respect to their vital action they are entirely recessive.

Aborted seeds.—In plants which are commonly self-fertilized, lethal factors of this kind are automatically eliminated soon after they occur; but in naturally cross-fertilized plants they can be perpetuated in the heterozygous condition and may remain in the stock for an indefinite period. In corn, where the seeds are produced in regular order on a central spike, whenever embryo abortion takes place and the ears are self-fertilized, the defective seeds are easily seen because they occur in definite proportions scattered uniformly over the entire ear, as shown in Fig. 172.

In this case, fertilization gives a sufficient impetus to start the development of the pericarp, which is maternal tissue surrounding the egg that later normally develops into the embryo and endosperm. This pericarp tissue grows to practically the same extent as if a normal seed were contained in it, so that the homozygous recessives are seen as completely empty or partially filled capsules interspersed among the well-developed grains. The distinction between the normal and defective kernels is usually so clear-cut that there can be no mistaking that this is the result of defective heredity. Aborted and defective kernels due to various causes other than heredity are found on many ears of corn, but there are seldom more than a few and they are rarely distributed evenly over the entire ear.

On wind-pollinated plants the defective kernels appear in small numbers and would be generally overlooked and considered as unimportant. Yet such vitally essential factors as these must have some weakening effect when in the heterozygous condition, and those plants which produce segregating ears are probably less productive, other influences being the same, than plants which are free from this defect. This form of sterility is probably one of the

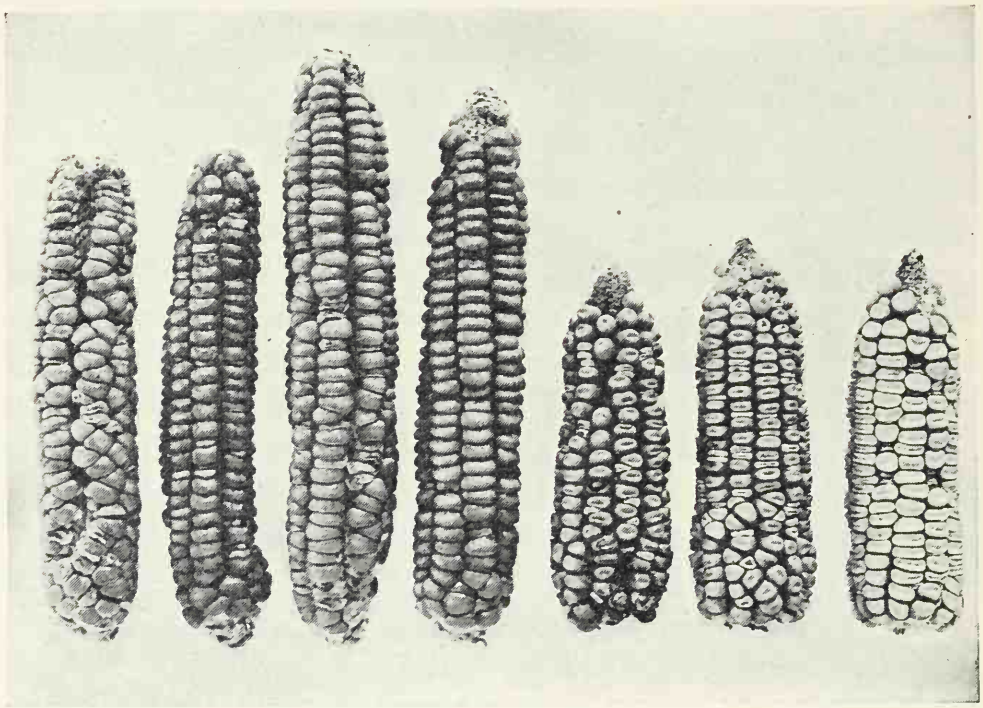


FIG. 172.—Self-fertilized ears of corn showing a recessive lethal character, aborted or defective seeds.

most common hereditary variations in corn, as it has been found to occur in all types from many different countries.

Embryo abortion in domestic animals.—Such factors as these have been recognized only in animals and plants with which experiments have been made. It is not unlikely that a similar condition exists in domestic animals and may be responsible for some of the abortions which frequently occur. This could not be easily detected in animals having single births. The low hatching percentage of eggs of the

hen and other forms of poultry may be due in part to recessive sterility factors of this kind.

Factors which limit reproduction.—Other recessive factors in plants permit normal development of the seed, but the seeds fail to germinate, or as soon as the seedlings start to grow they become abnormal in structure and soon die. Another type of inherited abnormality enables the seeds to be fully formed, but instead of going into the resting

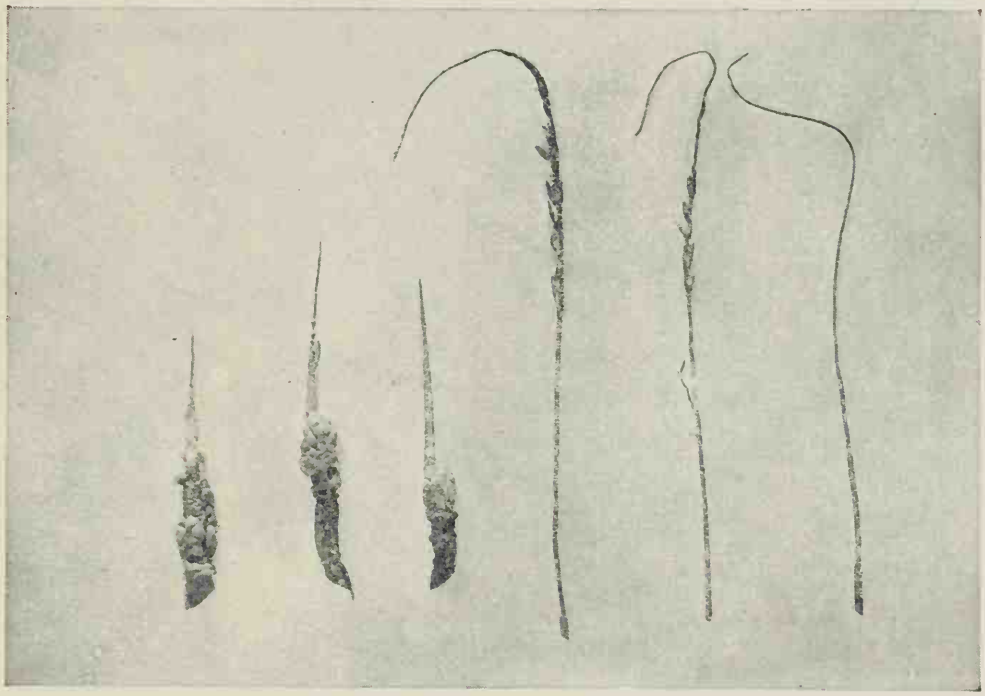


FIG. 173.—A sterility factor in corn, affecting both pistillate and staminate flowers.

stage at maturity they keep on growing. One-fourth of the seeds from a self-fertilized ear segregating for this factor sprout on the ear if conditions are suitable and soon die. The common albino seedlings which appear frequently in corn and many other plants are other examples of hereditary factors which stop development as soon as the food stored in the seed is exhausted.

After the plant passes the seedling stage, it ordinarily develops without manifesting many serious hereditary weak-

nesses until the organs for reproduction are being laid down. There are many illustrations of entire or partial derangement of the floral organs. A factor which almost entirely destroys both types of flowers of maize is shown in Fig. 173. Figs. 174, 175, and 176 show sterility of the staminate and pistillate flowers of corn. Similar occurrences have been reported in sweet peas, flax, and potatoes. In these, the

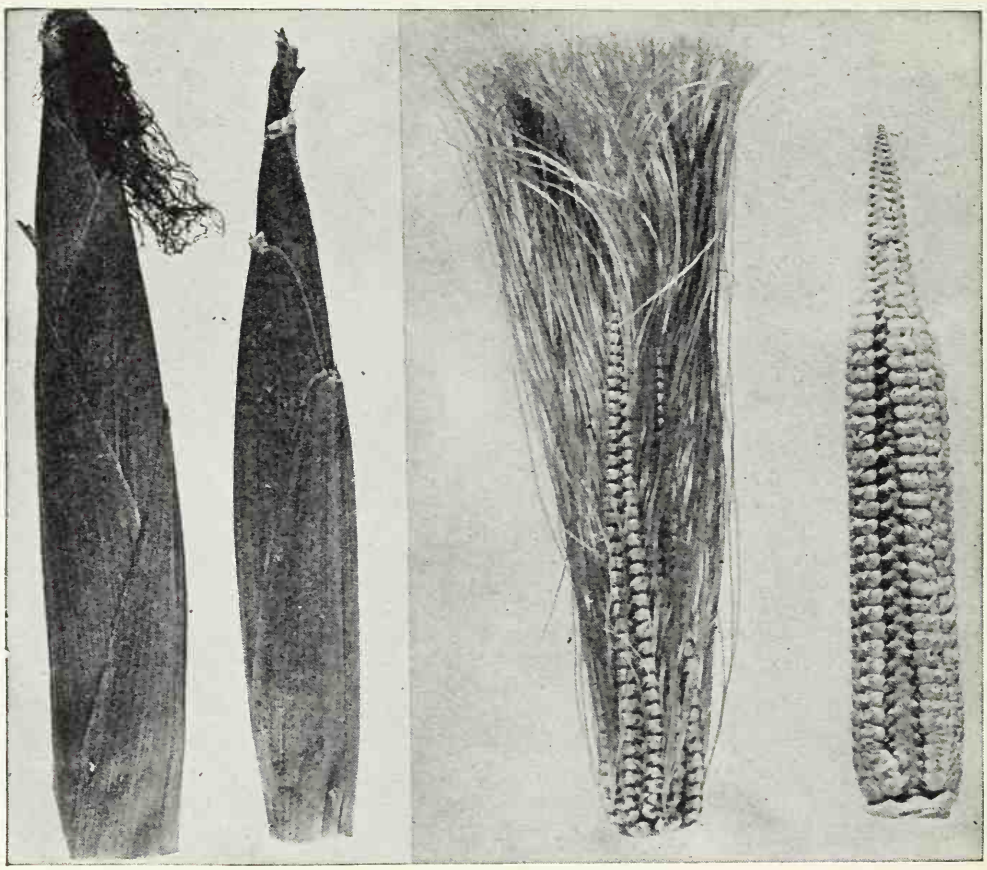


FIG. 174.—A sterility factor in corn, affecting only the pistillate flowers. A normal and silkless ear with and without husks.

anthers are defective and produce no viable pollen. In animals, fowls exhibit hereditary malformation of the reproductive organs. In most of these cases simple Mendelian factors are responsible for the sterility, and these are always recessive.

Although inherited defects may stop the growth of the plant or animal at any stage, most of the manifestations of

the effects of lethal factors center around the process of reproduction. This apparently is the critical time in the life history of any organism. At any time from the beginning of the development of the sex organs through the reduction division and maturation of the germ cells, until after fertilization and the start of the embryo in the following generation, something may go wrong and interfere with normal fertility.

Summary.—To sum up the facts of sterility, we see that

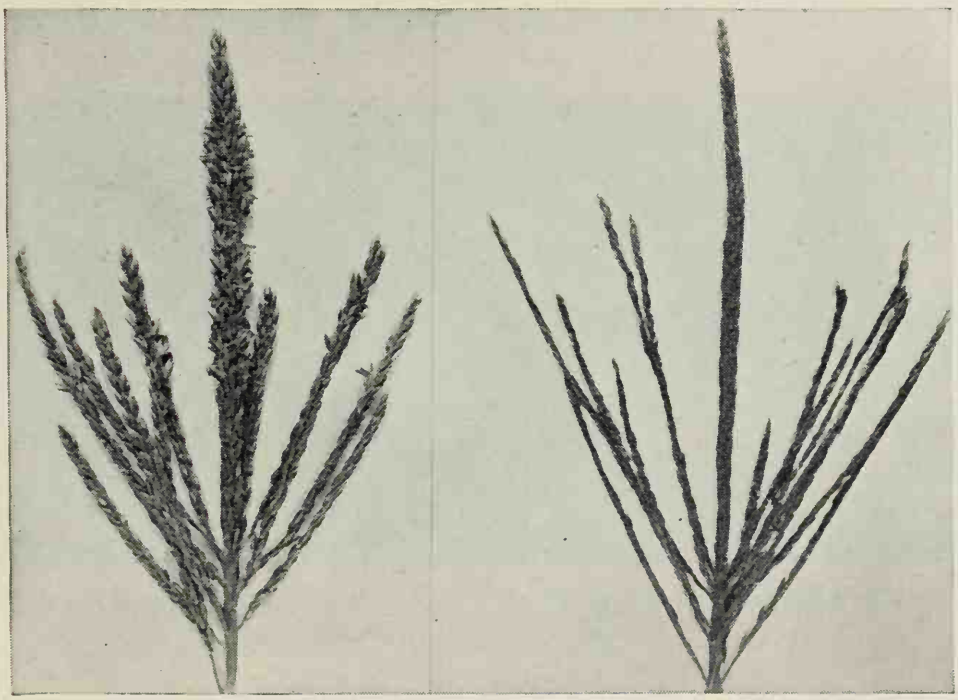


FIG. 175.—A sterility factor in corn, affecting only the staminate flowers. A normal tassel on the left. (After Eyster in Jour. Heredity.)

subnormal reproduction may result from influences outside of the organism, due to the diverse modifying external conditions in the plant's or animal's surroundings; but frequently sterility results from the expression of definite hereditary factors which are internal and have their basis in the germplasm.

Inherited sterility is of two kinds: incompatibility and impotence. Incompatibility within the species is not due

to any abnormality in structure and is a special function which operates to promote cross-fertilization. In economic forms of life, it is for the most part distinctly undesirable. Impotence is more variable in its expression. It results from structural derangement of various parts that are concerned directly with reproduction. In some cases impotence may have a relatively simple factorial explanation, while in others it is the result of the inharmonious interaction of very dissimilar germplasms brought together from widely different sources.

Sterility of the type of impotence comes to light most

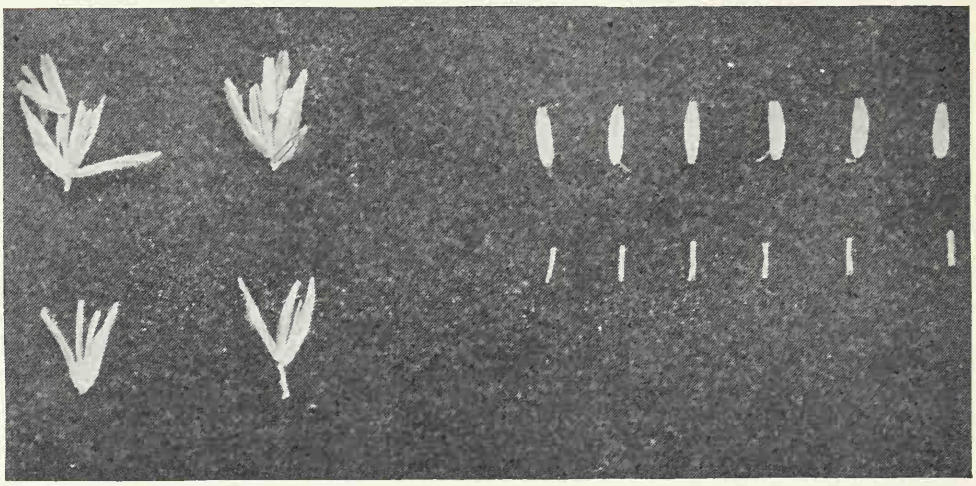


FIG. 176.—Normal and sterile spikelets and anthers from the tassels shown in Fig. 175. (After Eyster in Jour. Heredity.)

frequently when crossbred organisms are intensively inbred. We know that inbreeding is not responsible for their origin. The germinal influences which reduce fertility are many and complex and are still far from being adequately accounted for; but, as far as can be judged at present, many forms of sterility have their beginnings in hybridization. The bringing together of radically different forms of life, which has frequently occurred in the development of domesticated animals and plants, has left a large number of ill-adjusted and unstable combinations of germplasms. Defects which arise from improper adjustment have been masked, hidden from

sight, and perpetuated from generation to generation by constant crossing. Inbreeding brings them into visible expression. Only then can they be eliminated.

Obviously, inbreeding is the panacea for sterility of the type of impotence. Rigid and unvarying inbreeding of the most intense kind possible is the only certain cure for this serious handicap to plant and animal production. The remedy may, in some cases, be drastic; yet the results are sure. When the hereditary factors that cause sterility are once gotten out completely, they are out to stay. Vigor can always be restored by suitable crossing, and the result in the end may well be worth the effort.

Sterility due to incompatibility can not be eliminated in this way unless the hereditary factors for self-fertility are present in the material worked with or are introduced by crossing. The attempt to overcome this physiological barrier to full fertility by inbreeding, without having these facts clearly in mind, is not only certainly useless but will even increase the occurrence of the very trouble which it is desired to remedy.

CHAPTER XIV

METHODS FOR PLANT IMPROVEMENT

THE systematized facts about the occurrence of variations and the mode of their transmission from one generation to another form the basis for the science of genetics. Although a knowledge of heredity is essential to an understanding of the way in which domesticated animals and plants have been brought from the wild to their present usefulness, and is a direct help to still further progress, it should be remembered that plant and animal improvement by breeding is an art. One may have at ready command all that has been learned about heredity from the time of Camerarius down to the publication of the most recent treatise on the chromosomes as the carriers of the inheritance, but unless he has the enthusiasm and patience of a sculptor or a painter, there is small hope of his producing any meritorious new form of life. A first-hand familiarity with the material worked with is the primary requisite for successful plant breeding. Most of the great achievements in the past have come from those who knew little about the underlying principles of variation and inheritance. Improvement is still possible with no other tool than selection founded upon the rule-of-thumb that "like produces like"; but much wasted effort can be prevented, and the discouragement which follows the attempt to do impossible things can be avoided, by the use of the sound principles of genetics already learned. Moreover, many of our longest-cultivated plants have about reached a limit beyond which it is impossible to make any appreciable progress unless a radical change in method, based upon the proved principles which have followed Mendel's pioneer work, is brought about.

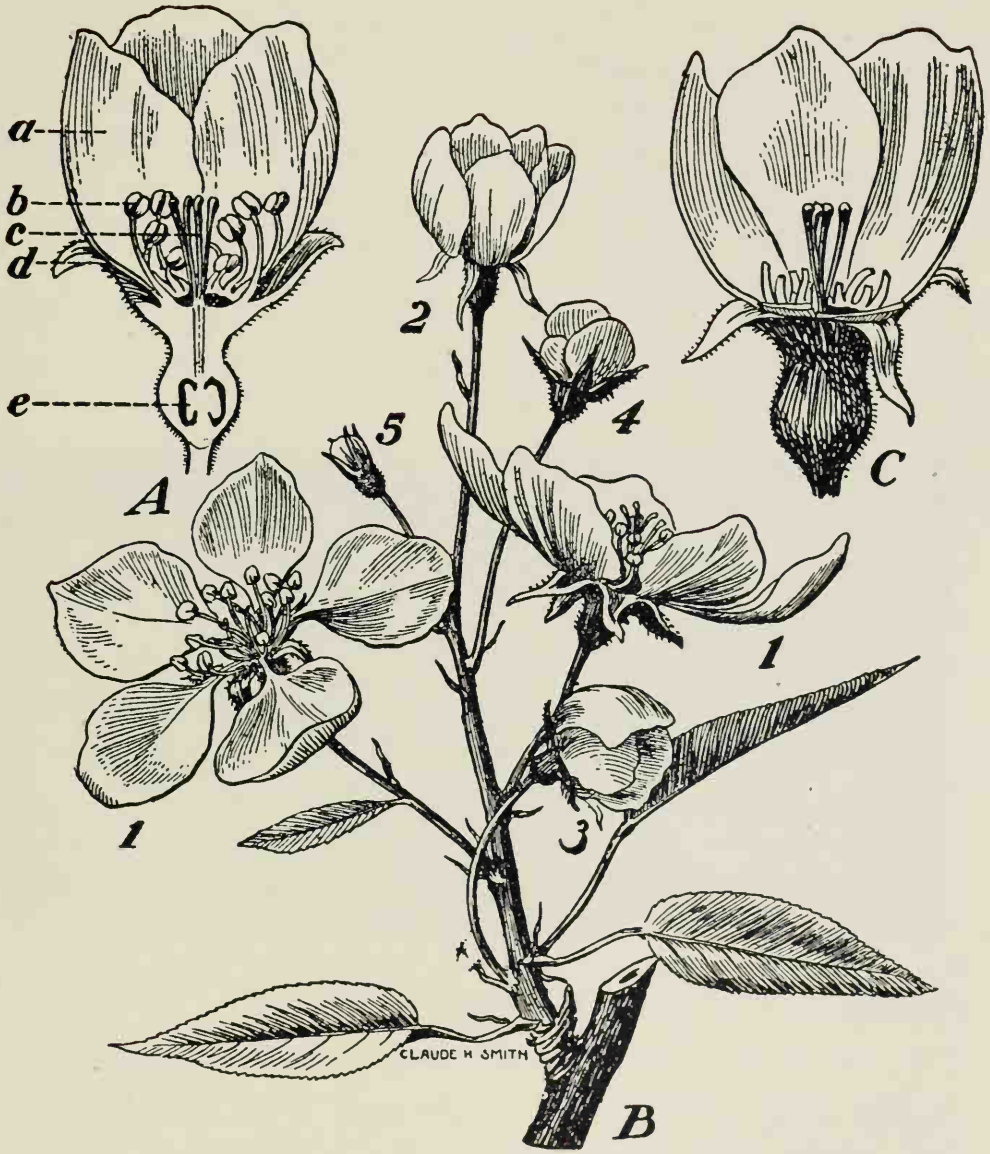


FIG. 177.—Technique of hand-pollination illustrated by the apple flower. A, section of flower showing *a*, petals; *b*, stamens with anthers containing the pollen; *c*, styles and stigmas upon which the pollen is deposited; *d*, calyx; *e*, ovules from which the seeds develop. B, spray of flowers; in *1* fertilization has already taken place, *2*, *3*, and *4* are ready to be emasculated, while *5* is too young. C, emasculated flower with stamens removed before pollen is shed, ready to be pollinated. (After Freeman in Kansas State Agr. College Farmers Institute Bull. vol. 1, no. 2.)

Artificial pollination.—Every plant presents its own peculiar problems. Since hand pollination is frequently employed, it is necessary to understand the floral mechanism, and this varies widely in different species. Some plants are easily handled and set seed abundantly when artificially pollinated, while others are extremely difficult to manipulate successfully. The best technique, in some cases, is mastered only after much practice.

Utilizing natural crosses.—For practical purposes it is sometimes better to depend upon natural crossing to bring

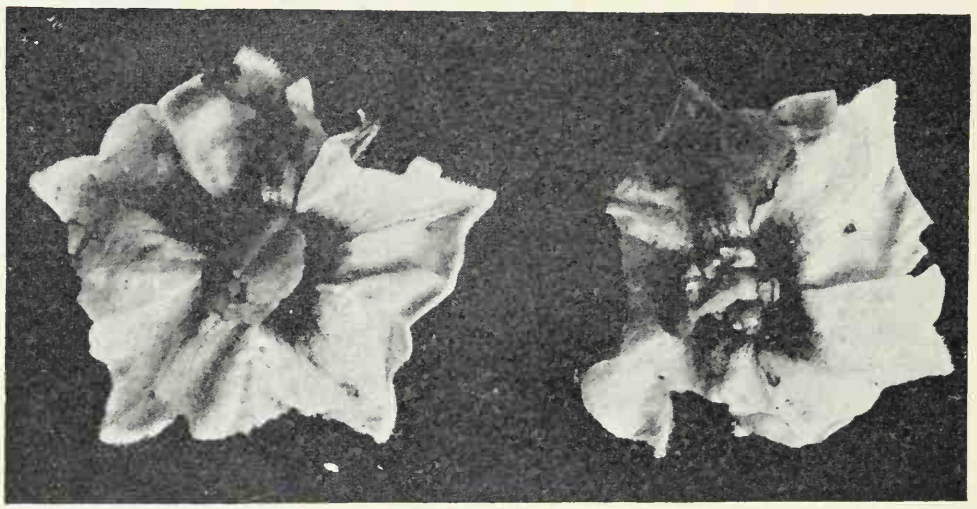


FIG. 178.—Potato flowers, before and after emasculation. (After Stuart in U. S. D. A. Professional Bull. 195.)

together plants which are artificially cross-fertilized with great difficulty. It is often easier, and equally satisfactory, to plant two different types close together and allow them to intercross naturally. Where the characters are such that the resulting hybrids can be distinguished from the seed parent, this method can be used with nearly the same degree of certainty as when the forms are artificially united. Soy beans, for example, have small and delicate blossoms, and these are so formed that emasculation is extremely difficult. Although cross-pollination takes place very rarely in this plant, it is easier to grow several hundred plants side by side

and examine their progeny the following year for hybrid plants, than to attempt crossing by hand.

Regulating the blooming period.—It is frequently found that plants which are to be crossed fail to blossom at the same time. When pollen can not be kept viable for a sufficient length of time, it is necessary to adopt some other expedient. Cuttings from the flowering branches of deciduous plants can be held in cold storage and forced into bloom to produce pollen at practically any time. By regulating the relative length of daylight and darkness, annuals and herbaceous shrubs can be greatly changed in their time of blooming. This opens up a large number of possibilities for bringing together new forms which have never before been crossed.

Mode of pollination.—In order to apply the right method, the first essential is to know how the plant is pollinated under natural conditions. Some plants are largely self-pollinated; others are almost wholly cross-pollinated. When inter-crossing has been going on continually, a condition is brought about whereby the plants are dependent upon cross-fertilization to maintain vigor and productiveness. Where self-fertilization is the rule, crossing is not needed to maintain vigor. Some plants are partly cross-fertilized and partly self-fertilized in their natural state. In fact, all gradations between the extremes of compulsory cross-fertilization and complete self-fertilization are met with. Many valuable plants are no longer propagated by seed, and a few are unable to produce seed under any conditions.

Classification of agricultural plants.—According to the usual mode of pollination, the principal cultivated plants can be arranged in two main classes, as follows:

I. Plants largely self-fertilized

Barley, beans, cotton, cowpeas, flax, oats, peas, tobacco, rice, sorghum, soy beans, tomatoes, wheat.

II. Plants largely cross-fertilized

A. Generally self-compatible

Alfalfa, corn, beets, and many annual flowers.

B. Partly or wholly self-incompatible

Cabbage and other crucifers, clover, timothy and other grasses, many fruits, melons and other cucurbits, rye, sunflower.

C. Dioecious plants

Asparagus, date palm, hemp, hops, spinach.

Those plants which are propagated vegetatively, such as the potato, sweet potato, sugar cane, nearly all fruits, most ornamental shrubs and vines, and many flowers, are all treated in much the same way and their normal mode of pollination is not important.

Amount of natural crossing.—Among the self-fertilized crops, variation occurs in the amount of natural crossing. About 1 or 2 percent of the plants of wheat and rice result from cross-pollination, but this amount varies with different varieties, seasons, and localities. Barley and oats are much less cross-fertilized than wheat. Soy beans are crossed only in a fraction of 1 percent of the plants. Tomatoes are crossed from 3 to 4 percent. The amount of natural crossing in cotton ranges from 5 to 15 percent, and in sorghum it may run as high as 50 percent.

Of the commonly cross-fertilized plants, corn is the best example. It is pollinated by the wind; the flowers are borne on different parts of the plant and often mature at different times, so that the conditions are favorable for a large amount of germinal mixing. Single white-seeded corn plants have been grown in fields of yellow corn, and less than 5 percent of self-fertilized white seeds were found on the ears. Although the flower of rye is similar to that of the other small grains, crossing is frequent in this plant,

being necessary on account of the self-incompatibility which it usually exhibits. Heribert-Nilsson found that 71 out of 73 plants of one variety were self-sterile, one was found to be partly self-sterile, while only one was fully self-fertile.

The flowers of alfalfa are so arranged that unless the petals are disturbed by insects or other agencies the pollen can not reach the stigmas and no seed will be formed. Bees and other large insects cause the flowers to burst open. The stigma and the anthers come violently in contact with the back of the insect receiving and depositing pollen at the same time.

The way in which flowers are formed, with regard to the mode of pollination, is not always a reliable guide to the actual amount of crossing. Tobacco is freely visited by insects; yet cross-fertilization takes place in not more than 2 or 3 percent of the plants, as shown by Howard and others in India. The amount of crossing can be determined in two ways:

Plants which differ in visible characters can be grown near each other, and the number of off-type plants which segregate in their progenies can be noted in the following generations. Also, by self-fertilizing individual plants and observing the uniformity, some idea can be obtained of their customary mode of pollination. If self-fertilization is the rule, the offspring will generally be true to type, and will show small variations and no marked reduction in size or vigor. Frequent crossing in cultivated plants is practically certain to result in many heterozygous plants in the population, which when self-fertilized will give variable progenies usually with lessened vigor.

Variation in self-fertilized plants.—Since self-fertilization automatically reduces heterozygosity, and differences in productiveness always result in the propagation of the most fertile types and elimination of the others, all largely self-fertilized varieties will tend to be uniform and stable and composed of individuals which are alike in their heredi-

tary constitution. But there is always the possibility of some crossing between different sorts, and mechanical mixing also frequently occurs in threshing the seeds, in handling in the storehouses, and, where different varieties are grown on the same field in successive years, in seeds living over in the soil. Spontaneous germinal changes may also take place and, although they are rare in occurrence and are seldom of value, they present a possibility which must be taken into consideration. Every variety, unless it has been recently purified, contains a number of different types. Each is breeding true to its own type but, like all living organisms, shows fluctuating variation according to the conditions in which the individual plants are grown.

The method of breeding self-fertilized plants is simply to separate these elementary varieties and to pick out those strains originating from single individuals which are the most suitable for the purpose desired and propagate only from these. This is generally known as the pure-line method of breeding. The procedure varies with different crops, but the principle involved is the same for all and is based upon the fundamental fact that the genetic constitution of any individual can only be known accurately by the behavior of its offspring. In order to distinguish between transitory modifications due to the environment and the permanent variations due to germinal changes, the progeny performance test is the criterion by which selection is made.

History of the development of the pure-line method.— This method of carrying on selection, based upon the descendants of single individuals as a group, has been slowly developed. The first record of single-plant selections methodically carried out was shortly after 1800. On the Island of Jersey there was a farmer by the name of Le Couteur, who was interested in the improvement of his crops. A visitor from Spain, Professor La Gasca, from the University of Madrid, pointed out to him that his wheat field, instead of being uniform and pure as Le Couteur had supposed, contained a number of types which differed

in appearance, and he suggested that they might also differ in productivity and milling quality. This induced Le Couteur to pick out a number of different heads of wheat, and these were grown separately the following year. The uniformity within each type was noticeable. While most of the selections were no better than the mixed variety from which they came, a few appeared to be superior. These were tested further. Some of them were good enough to be named and widely distributed, and one variety, Bellevue de Talevera, is said to be still grown and popular in parts of England and northern France.

At about the same time, a Scotchman, Patrick Shirreff, followed practically the same plan. He examined his wheat fields during the growing season, and when an exceptionally strong and vigorous plant was noted this was marked and the seed saved separately. These were kept distinct, increased in amount, and tested, and this finally led to the production of a number of named varieties which gained a wide reputation. The same procedure was applied to oats.

Hallett began working with wheat, oats, and barley, about 1857, and followed a radically different plan. He believed, as was generally held at that time, that those characters of the plant which were induced by favorable cultural conditions would be transmitted, and even thought that the different heads on the same plant and the different seeds within a single head had the power to pass on their good qualities. His plan was to raise his plants under the best possible growing conditions and select the best seeds from the largest heads on the strongest and most productive plants, year after year. In this way he hoped to get a continued improvement. His results showed that in some cases he did get an increased yield. Hallett's success was more probably due to the sorting out of genetically superior strains at the first selection, and not to a gradual improvement as he assumed, unless in some cases he was working with recently crossed plants. A number of named

varieties were put out, among which Chevalier barley has proved to be very valuable.

The Vilmorins, in France, practiced selection with a large number of plants in connection with their seed business. Considerable attention was given to the sugar beet, and they soon came to the conclusion that the greatest progress resulted from single-plant selections when their progenies were grown and compared under equal conditions. This conclusion was later reinforced by their observation with other material, wheat, that fifty generations of selection in the descendants of a single plant were unable to make any appreciable change in the character or productiveness of this plant, as noted in Chapter IX.

Plant breeding in Sweden.—In 1886, the Swedish Seed Association was formed, with headquarters at Svalöf, for the purpose of developing higher yielding and more uniform varieties of cereals and legumes. At that time it was still generally believed that the variations due to soil and season tended to be transmitted to the following generations, and that selection of these variations would result in continued improvement. This was the result of the widespread acceptance of the Darwinian doctrine of natural selection. Setting to work, they carefully examined fields of wheat, barley, oats, peas, and vetches for the strongest and most productive plants. A large number of such plants were taken from each variety, harvested together, and their seeds bulked in one lot, forming an elite stock for planting the following year.

Selection was carried on in this way, year after year. Attention was paid to selecting plants which conformed to fixed standards even in minor structural details, so that even by this mass selection considerable uniformity was brought about and an appreciable improvement was made in ability to yield and in winter hardiness.

After the selection had been carried on in this way for five years, Hjalmer Nilsson, who then took charge of the work, noted that even the most carefully selected varieties

still differed in many minor details, such as shape of spikes, color of glumes, and amount of pubescence. He then carefully separated the varieties into as many types as he could make, using the smallest details as the basis for classification. It was found that a few plants were unlike any other plants in the same selected variety. Other types contained many plants all exactly alike as far as could be seen. Each type was planted separately, and at harvest it was observed that of all the hundreds of cultures, only those few which came from a single plant produced a uniform progeny. All the others were variable in respect to some characters. They concluded that the quickest way, if not the only way, to obtain a uniform variety of self-fertilized crops was to make the single plant the basis for selection. This method was followed from then on and has been applied on a very extensive scale. All their experience shows that everything depends upon the inclusion of potentially valuable individuals among the original individual plant selections, and that subsequent selection among the descendants of these isolated plants, if they give uniform progenies at the start, is almost wholly without avail. To-day the most successful varieties grown in Sweden are the outcome of this system of selection.

The justification for the adoption of the system of single-plant selection was at once realized when Mendel's work led to Johannsen's development of the genotype conception, following Weismann's demonstration of the stability of the inherited germplasm and its insulation from ordinary environmental influences.

Methods used at the Minnesota Station.—While the importance of the individual as the unit of selection was being demonstrated at Svalöf, W. M. Hays at the Minnesota Station, in 1892, grew 400 plants of Blue Stem wheat in single hills about 1 foot apart. Several plants taken from this lot yielded above 500 seeds per plant and weighed 10 grams or more. Starting with these promising plants, seed of each was increased as rapidly as possible in separate

plots until enough was obtained to test them in drilled fields. The best of these, chosen on the basis of yield from large plots, were found to yield from 1 to 2 bushels more than the original variety.

The centgener system.—The system used by Hays became generally known as the **centgener** method, because the plants were handled in multiples of 100, for convenience. The number is of no particular importance, but the plan independently arrived at was essentially the same in prin-

FIG. 179.—Rows of wheat, each of which is planted with the seed from a single head. (After Love in Jour. Heredity.)

ciple as the method developed in Sweden and later applied extensively throughout Europe.

Hays' method of procedure was to select a large number of individual grains having the desired size, texture, and appearance, from a mass lot of seed of the variety to be worked with. Usually 1000 were taken and planted singly 1 foot apart. The outside rows and those bordering on intersecting paths were planted with some uniform variety, to be discarded, in order to guard against uneven growing conditions. At harvest, 100 of the highest-yielding and

otherwise most desirable plants were selected and 100 seeds of each were planted in a small plot the following

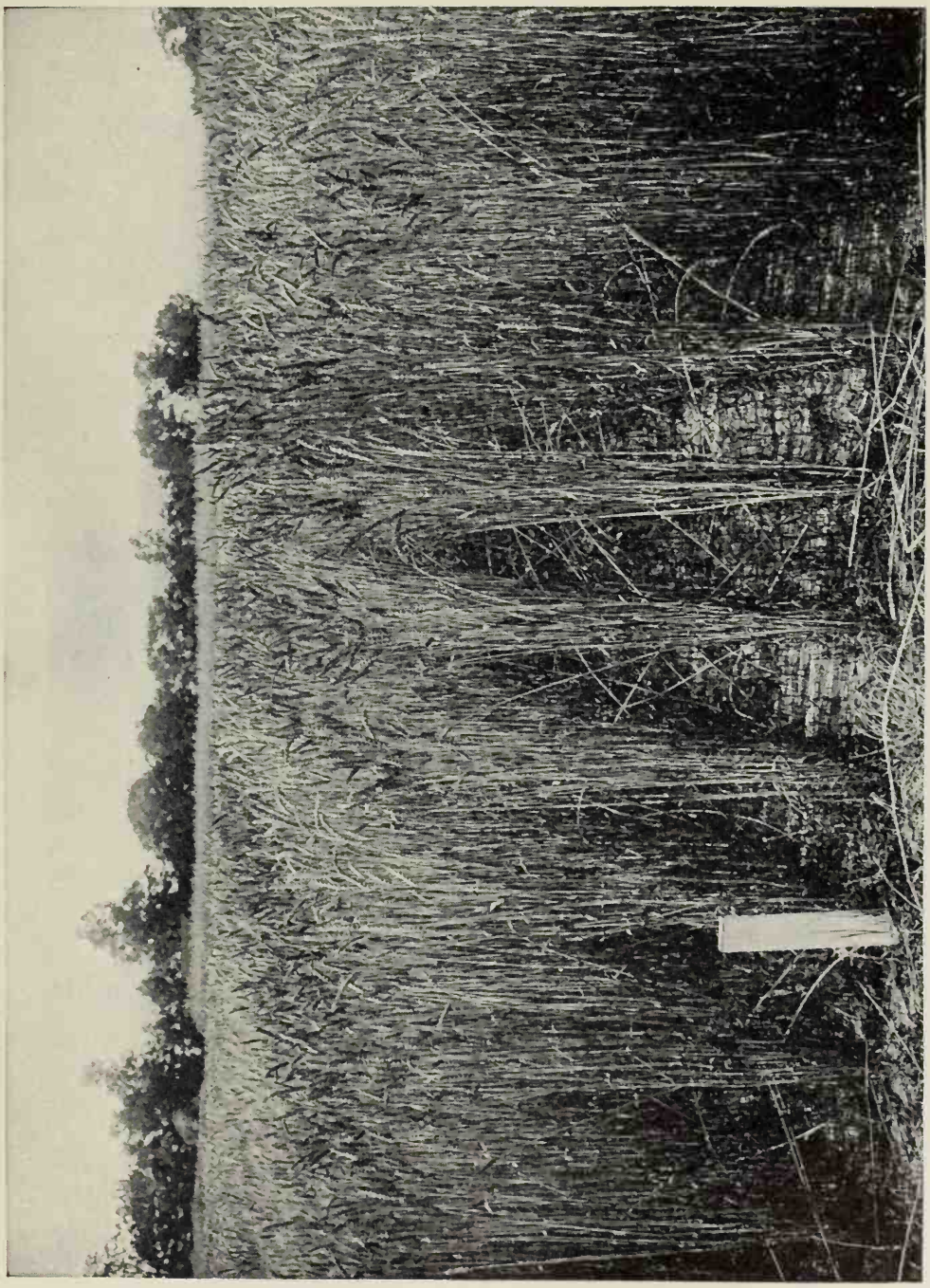


FIG. 180.—Rod-row plots of wheat planted with the seed from the best single-head selections as tested the previous year. (After Love in Jour. Heredity.)

year. From these, the best were again selected and increased as quickly as possible, until the final eliminations

were made on the basis of the yield of fairly large drilled plots.

Cereal breeding methods.—A modification of this system is now in more general use. Instead of starting with single seeds, individual heads are selected in the field. Since each represents a single plant, a larger amount of seed is available at the start. These are grown in short rows, which sometimes alternate with check rows planted with some uniform lot of seed of one variety. Barley or rye is often used as a check for wheat, to guard against possible

FIG. 181.—Increase plots of wheat the following years, at the Cornell University Agr. Exp. Station. (After Love in Jour. Heredity.)

crossing. All promising head-row progenies are increased as rapidly as possible, and final choice is made on the basis of yield and behavior with respect to all important features. The tests are repeated for many seasons, and the plants are grown in good-sized plots.

This method with modifications is also used with oats, barley, and rice, and the same principle is employed with beans, peas, and all self-fertilized crops. Nearly all the experiment stations in the grain-growing districts, together with the United States Department of Agriculture and some private individuals, are applying this method of

breeding to the small grains. Already a number of named varieties, each of which represents the descendants of single plants, have been widely grown.

Production of Kanred wheat.—One of the most successful of these, in point of acres grown, is the Kanred variety of wheat produced by the Kansas Station. Since the development of this valuable wheat is representative of the application of the pure-line method to the improvement of self-fertilized plants, the history of its production will serve as a good illustration of the methods used.

In 1906, H. F. Roberts made 554 single-head selections from Crimean, a variety that had been introduced from Russia in 1873. Each head selection was grown in a short row alternating with a check row of Kharkof, a uniform, well-adapted, high-yielding wheat. All were compared with the adjoining check rows for earliness, winter-hardiness, disease-resistance, lodging, quality of grain, and yield. By 1908, all but 122 of these had been discarded as inferior. Beginning in 1911, the more promising lines were grown in one-tenth acre field plots, whereby more accurate tests on yield could be secured. Milling and baking tests and chemical analyses were also carried out and used in making the final selection. In 1914, after eight years of preliminary testing, Kanred was grown in various parts of the state in coöperative tests with farmers. Since that time its acreage has increased rapidly, from about 4000 acres in 1917 to approximately 2 million acres in 1921.

Qualities of Kanred wheat.—The line finally chosen as the best ripens earlier than the leading varieties commonly grown, by as much as four days in some seasons. The difference is sometimes not as marked as this, but even a small difference is very important in a region of limited rainfall. Kanred is also resistant to winter injury, which is of great importance in a region where the damage from this cause may amount to as much as 50 percent of the crop. In a year of severe injury, the selection yielded 19.2 bushels per acre in comparison with 13.2 and 11.9 for Turkey and

Kharkof. Much of this difference is attributed to increased winter-hardiness on the part of Kanred. Observations in the field and inoculation experiments have also shown that this new wheat is markedly resistant to certain kinds of black-stem and orange-leaf rust. All of these qualities, together with others that can not be so easily recognized, enable Kanred to yield appreciably more on the average than any other kind of wheat, of equal quality for bread-making purposes, grown in the hard winter wheat region. The yield of Kanred in comparison with standard varieties for a period of twelve years is given in Table XXXIX.

TABLE XXXIX

COMPARISON IN YIELD OF KANRED AND OTHER COMMONLY GROWN VARIETIES OF WINTER WHEAT IN THE CENTRAL PLAINS AREA

Data from Parker

Year Grown	Yield in Bushels per Acre			
	Crimean	Turkey	Kharkof	Kanred
1911	28.9	31.1	26.1	34.6
1912	13.0	13.2	11.9	19.8
1913	37.7	33.6	33.8	37.1
1914	37.7	36.1	36.0	35.2
1915	21.5	23.0	22.9	26.0
1916	22.6	22.2	24.6	33.6
1917	10.5	12.7	14.6	16.6
1918	18.0	16.3	16.9	21.7
1919	21.0	20.7	22.9	20.7
1920	28.9	29.3	29.1	31.3
1921	28.2	31.0	31.0	33.1
Average	24.4	24.5	24.5	28.1

Kanred the product of introduction and breeding.—Since the plant that finally came to be named Kanred was one among a variety originally introduced, it is possible that this is partly an instance of a valuable plant introduction rather than an improvement brought about by selection.

In other words, the introduced variety may have had the same superior qualities that the plants taken from it were found to have, just as a newly introduced variety of rye from Russia, known as Rosen rye, discovered and tested by Spragg at the Michigan Station, has been found to have superior yielding qualities for certain sections. It is not the result of pedigree selection but apparently developed its superior qualities in other lands.

Unfortunately, there are no tests comparing Kanred

FIG. 182.—Harvesting rod-rows of oats at the Cornell University Agr. Exp. Station. (After Love in Cornell Bull. 343.)

directly with the original stock from which it was derived. However, this introduction of Crimean wheat was tested by the United States Department of Agriculture in comparison with the standard varieties of hard red winter wheat and was discarded because it showed no superiority over these varieties. Tests carried out at the Kansas Station show that Kanred outyields all the commonly grown strains of Crimean wheat, so there seems to be little doubt that Kanred is the result of careful selection and testing.

Nevertheless, the importance of exhausting the possibilities of plant introduction before spending time and

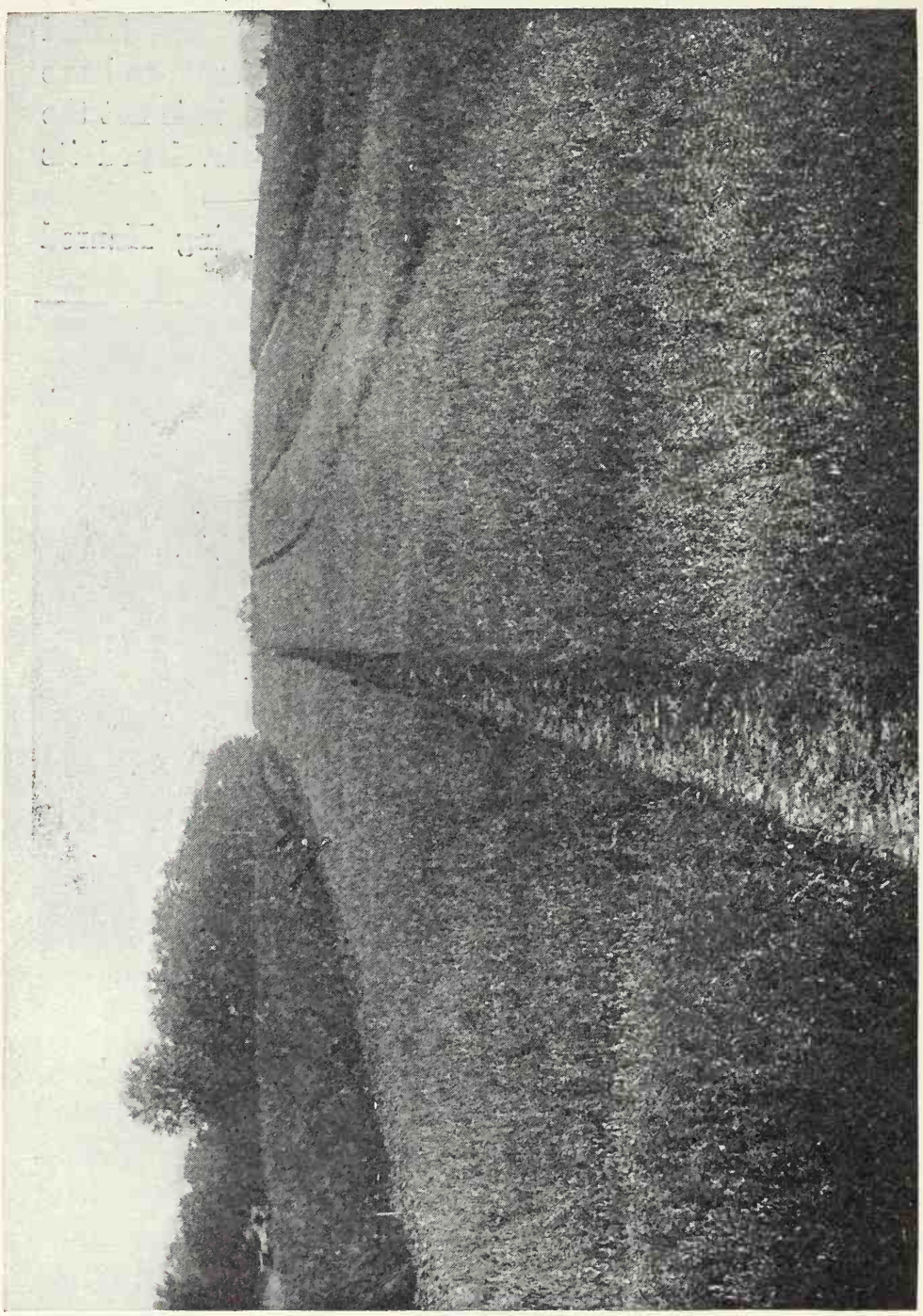


FIG. 183.—Oat-breeding plots at the Cornell University Agr. Exp. Station. (After Love in Cornell Bull. 343.)

effort upon material which may not be the best to start with, should be emphasized. It is unusual, however, to

find that a recent introduction is fully adapted to the new conditions, and the greatest possibilities lie in hybridization either among already adapted and proved varieties or between them and newer varieties which have some qualities of outstanding merit.

Hybridization applied to self-fertilized plants.—When applying hybridization to self-fertilized plants, the procedure is much the same as in making pure-line selections from fixed varieties after the cross has been made. If the stocks which are crossed are uniform, only one cross need be made and only enough plants of the first generation grown to produce seed for a large second generation. Since the maximum variability is brought about in the second generation, as has been shown from the operation of Mendel's law, it is the second generation that demands the closest attention. Practically every plant there will be the progenitor of a new variety, which may differ in some degree from all the others. Particular effort should be made, therefore, in this generation, to find those plants which have the most promise. Their progenies must be grown for several years and self-fertilized until they are uniform and stable. This takes about six generations on the average. Unlike the selections from fixed varieties, the strains following a cross will be changeable, and therefore rigid selection toward the desired standard must be kept up until the reduction in variability has ceased. After that, the most promising selections have to be tested for a long enough period to clearly establish their possible superiority.

Crossing, followed in this way by selection, has been extensively employed in the production of new varieties of wheat and many other crops, as stated in Chapter X. The procedure can be well illustrated by the production of a new variety of tobacco at the Connecticut Station, by East and Hayes.

Hybridization in tobacco.—The tobacco grown in New England is used almost exclusively for cigar wrappers. It is highly essential that the crops be uniform in quality, color,

and texture, and for that reason the types which are commonly grown have been carefully selected for uniformity. This is favored by the fact that tobacco is almost entirely self-pollinated. From time to time, seed is saved from single bagged plants, and one plant makes an enormous number of seeds. For these reasons, and because only a few varieties are grown and these in large acreages, for the most part, there is little opportunity for crossing between different sorts. Tobacco varieties are usually quite uniform

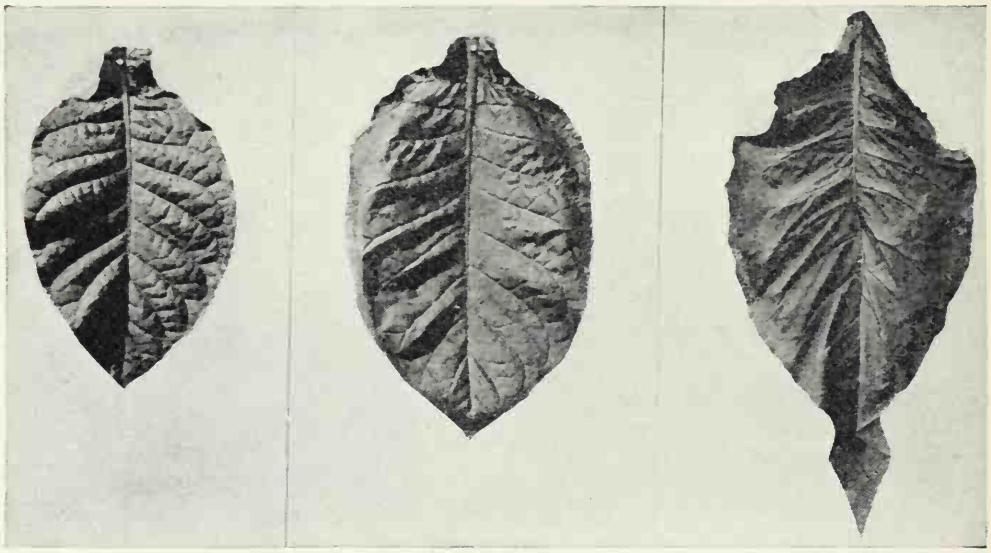


FIG. 184.—A representative leaf from two long-established varieties of tobacco, Sumatra (left) and Broadleaf (right), and a new variety Round Tip (center) obtained by crossing followed by selection.

and constant. Isolating and testing individual plants, which has given such valuable results with cereals, therefore offers a rather small chance for a marked improvement of tobacco. However, appreciable results have been obtained by Johnson in Wisconsin, Valleau in Kentucky, and others working with tobacco, particularly for resistance to disease. In this case, resistant plants are readily detected by their larger growth when the tobacco is grown on soil that is heavily infected.

None of the existing varieties of tobacco grown in New England adequately meet all the requirements of the

grower, manufacturer, and consumer. The ideal type of tobacco must be a strong grower, stand up stiffly throughout the season, hold its leaves erect to avoid breakage, and produce a large number of leaves close together on the stalk. The manufacturer desires a leaf that is broad and rounding at the tip, as this part of the blade gives the best wrappers. The leaf must not be too large or too small; neither so thick that the yield of wrappers per pound of tobacco is low, nor so thin that they will break. Color, texture, and flavor are difficult to describe, but the requirements are exacting.

Investigation showed that two varieties, Sumatra and Broadleaf, possessed practically all of these desired qualities between them, although each was lacking in several respects. The problem was to bring together as many as possible of the desirable qualities in one type. The following are the characters of the two varieties selected for crossing and the qualities desired to be brought together in one plant:

Broadleaf	*Sumatra*	*Prospective Type*
large leaf	small leaf	medium-sized leaf
narrow tip	round tip	round tip
drooping leaf	upright leaf	upright leaf
leaves close	leaves apart	leaves close
texture coarse	texture fine	texture intermediate
leaves thick	leaves thin	leaves intermediate
flavor good but strong	flavor none	flavor intermediate
yield high	yield low	yield high

The production of Round Tip tobacco.—The two varieties were crossed, and a few plants of the first hybrid generation were grown and self-fertilized. These plants were all alike and intermediate in comparison with their parents, tending somewhat toward the Sumatra type. The plants were vigorous, but the leaves were coarse-veined and of very poor quality. Six thousand plants of the second generation were grown. These showed the greatest variation, exceeding the upper limits of the most leafy parental variety in number of leaves, and also surpassing the roundest leaved variety in breadth index (breadth ÷ length) as brought out

in Tables XL and XLI. The diversity in height of plant, size, texture, and color of leaf was equally pronounced.

FIG. 185.—A new variety of tobacco re-established by self-fertilization following a cross of two different types.

FIG. 186.—Diverse types of tobacco obtained from the cross of Little Dutch and Cuban tobacco. (After Johnson in Genetics.)

The opportunity for recombination in tobacco is shown strikingly in the accompanying illustration of a somewhat similar cross made by Johnson at the Wisconsin Station.

TABLE XL

FREQUENCY DISTRIBUTION OF THE NUMBER OF LEAVES PER PLANT OF THE CROSS OF SUMATRA AND BROADLEAF

Data from Hayes, in Connecticut A. E. S. Bull. 171

Generation	Number of Leaves per Plant																		Total	Average	C. V.
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34			
Sumatra	..	..	..	..	...	...	...	3	13	27	25	21	16	15	4	1	..	..	..	125	26.5±.11	6.6±.28
Broadleaf	2	9	22	39	22	11	3	...	...	...	..	..	..	..	..	..	..	..	..	108	19.1±.08	6.5±.30
F_1	..	..	..	2	0	3	21	47	38	29	10	..	..	..	..	..	..	..	..	150	23.6±.07	5.5±.21
F_2	..	2	13	58	132	263	332	313	246	150	67	29	14	4	4	2	1	1	1	1632	22.7±.03	9.0±.11
F_7	..	..	..	..	..	..	..	..	..	3	7	9	17	22	18	13	7	3	1	100	29.1±.13	6.6±.31
F_7	..	..	..	..	..	..	..	1	6	19	24	35	15	..	..	..	..	..	..	100	26.3±.08	4.5±.21
F_7	..	..	..	..	..	..	..	3	3	7	17	20	18	13	8	7	3	1	..	100	27.7±.14	7.6±.36

TABLE XLI

FREQUENCY DISTRIBUTION OF BREADTH INDEX OF LEAVES OF THE CROSS OF SUMATRA AND BROADLEAF

(Data from Hayes, East and Beinhart, in Connecticut A. E. S. Bull. 176

Generation	Breadth Index												Total	Average	C. V.
	36	39	42	45	48	51	54	57	60	63	66	69			
Sumatra	..	..	..	2	15	47	43	30	12	1	..	..	150	53.5±.19	6.6±.26
Broadleaf	..	2	13	41	46	32	13	3	..	..	..	..	150	47.9±.20	7.6±.30
F_1	..	..	..	5	15	34	62	28	6	..	..	..	150	53.2±.18	6.2±.24
F_2	1	2	9	21	30	15	16	9	2	1	0	1	107	49.3±.35	10.8±.50

Among the 6000 plants of the segregating generation of the cross of Sumatra and Broadleaf, 20 were selected as coming nearest to the type sought for, as far as could be judged from the growing plants in the field. These were self-fertilized, and from 1 to 300 plants of each were grown the next year. The leaves of the progenies were harvested separately, cured, and sorted. The number of leaves and growth character of the plants were noted in the field, and the most desirable individuals in each lot were again self-fertilized. This procedure was continued for six years. During that time the poorer selections were discontinued,

as they failed to come up to the others in yield or quality of the cured leaves, until finally 3 of the best remained. These were grown in one-third-acre plots for three years, and final choice was based on the weight, quality, color, shape, and texture of the cured leaves during these successive seasons. The resulting variety was named Round Tip and distributed to the growers for extensive trial.

While it is yet too soon to decide whether this new variety has won for itself a permanent place in New England tobacco culture, it is sufficient for our purpose to know that this tobacco recombines in a large measure the desirable qualities of both parental varieties. It is actually a plant made to order from specifications which were drawn in advance. It possesses all the characters sought for at the start, with the exception that the leaves are placed too far apart to permit satisfactory harvesting by the method known as stalk cutting.

Uniformity and stability of hybrid recombinations.—From the theoretical standpoint, this experiment in hybridization, followed by selection, demonstrates the possibility of attaining a new variety that is as uniform and stable as the varieties started with. Many tobacco hybrids had been made previously, but had not been inbred and selected long enough to secure complete fixity. Having been distributed while still in a partially heterozygous condition, they have split up, to the disappointment and disgust of of those who grew them. This has resulted in a rather general conviction, among tobacco growers in particular because uniformity with them is of the utmost importance, that it is impossible to fix a hybrid. From the results of inbreeding given in previous chapters, this view is clearly not well founded. Only in a few exceptional cases do chromosome aberrations, lethal factors, or the selection of certain characters which are dependent upon the heterozygous condition, prevent the ultimate attainment of complete homozygosity.

The frequency distribution of number of leaves and the

coefficient of variability of the two parental races of tobacco and three of the inbred selections in the F_7 generation are shown in Table XL. The uniformity in leaf number was equaled by that manifested in other characters, as far as observation in the field could show, and this uniformity has remained constant as would be expected in continued self-fertilization.

Back-crossing.—In originating new varieties by hybridization, the value of back-crossing should not be overlooked. In many cases, a long-established variety has many desirable characters and is objectionable in only one or a few respects. When it is crossed with another variety, the chance of obtaining individuals which retain all of the original characters of the one variety, with one or a few characters replaced by others more desirable, is very small, and is only possible at all by growing large numbers. By repeatedly back-crossing the hybrid individuals in the second or later generations to the desired parental type, it is comparatively easy to restore the original set of characters and by selection to substitute certain more desirable qualities. Harlan and Pope call attention to the value of back-crossing and give as an illustration the results from their attempt to change a valuable variety of barley, Manchuria, to a smooth-awned type, at the same time retaining as much of the productiveness, quality, and general type of the former variety as possible. After crossing with a smooth-awned variety, a homozygous segregate in the fourth generation was back-crossed to Manchuria, and this back-crossing was repeated three times more. In this way a smooth-awned variety was obtained that looked more like Manchuria than any obtained previously, and no large number of plants were grown. Linkage tends to prevent the complete restoration of one parental type with single characters substituted, but as long as breaks in the linkage occur this goal can be more and more nearly reached. Back-crossing has long been used in animal breeding but has not received the attention it deserves in plant breeding in recent times.

Partially cross-fertilized plants.—Those plants which are partially cross-fertilized but are usually not appreciably reduced in vigor when artificially self-fertilized, such as

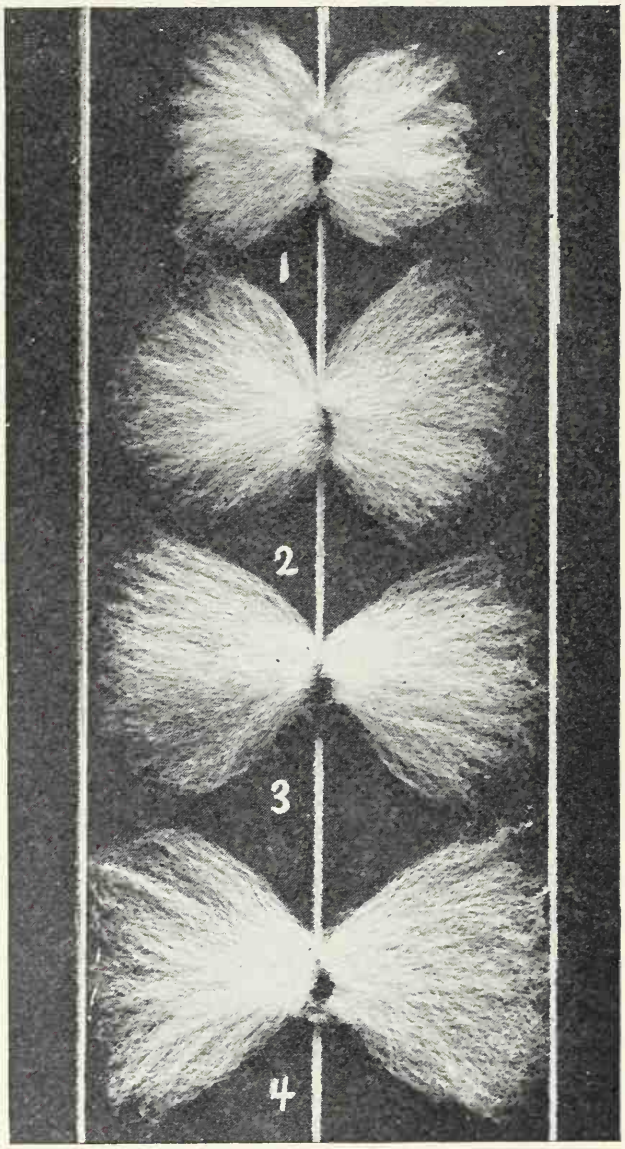


FIG. 187.—Progressive change in the fiber length of cotton resulting from single plant selections. (1) Mit Afifi introduced from Egypt, (2) strain of Mit Afifi after three years of selection, (3) Yuma, (4) Pima. (After Kearney in Jour. Heredity.)

cotton and sorghum, are handled in the same way as the naturally self-fertilized plants. The small amount of intercrossing always going on makes such plants somewhat more

variable, and care must be taken to prevent deterioration by mixing with other varieties. This necessitates continuous selection of the plants for the seed stock and roguing of fields used for general seed production.

Pima cotton.—The importance of this continued selection and roguing is well brought out by Kearney, in the production and maintenance of the Pima variety of long-staple cotton. Pima cotton is widely planted in the irrigated valleys of the Southwest. Approximately 250,000 acres were grown in 1920, all of the plants raised being the direct descendants of one plant selected in 1910 from a variety known as Yuma. This variety in turn was the result of a single-plant selection from cotton introduced from Egypt under the name of Mit Afifi. The selection in each case was based upon the uniform excellence of the progeny as well as the exceptional appearance of the mother plants themselves. The Pima selection came true to type from the start and has proved to be less variable than the original Yuma variety. None of the plants in the earlier generations were bagged for self-pollination, but the indications are that very little natural crossing took place.

For several years, a single plant was selected and used as the progenitor for each generation. As the successive generations proved to be uniform and reproduced the parental type, seed was rapidly increased in amount and used for field planting. The fields from which the bulk seed was obtained were isolated from other varieties of cotton, each plant was examined, and all off-type, weak, and unfruitful individuals were rogued out. From 1916 to 1920, an estimated total of over 3 million plants were examined, and the percent of plants removed each year was as follows: 0.21, 0.42, 0.20, 0.20. Most of the plants culled out were minor variations, probably due to poor growth, but a certain proportion of off-type plants, differing from the normal in habit of growth, foliage characters, and shape of boll, regularly appeared. These variations were usually heritable, as shown by progeny tests. They were similar to variations

occurring in the parental variety from which the Pima cotton was derived, but were less numerous in the new variety.

In 1919, two strains, one from a series of continuously open-pollinated plants and the other from self-fertilized plants, were compared with plants grown from seed of the original Pima plant. The variability of these three lots was calculated from data on twelve measurable characters pertaining to leaf, boll, seed, and fiber. Plants from the original stock were appreciably more variable than the two lots which had undergone nine generations of selection. The self-fertilized strain was less variable than the open-pollinated strain in only two of the characters measured, and was significantly more variable in one.

Origin of variations in cotton.—The abrupt departure of the Pima, Yuma, and other varieties isolated from Egyptian cotton (Fig. 188), and the fact that they breed comparatively true from the start, with no intergrading forms, causes Kearney to believe that they are not due to previous crossing with other varieties but are the result of mutations. It is considered by some authorities that Egyptian cotton originated as a species hybrid, and it is possible that the variation now taking place is the continuation of a complex segregation which has not yet been completed. The marked changes in many parts of the plants are not usually found in single factor mutations, and multiple factor mutations would not be expected to take place at the same time in the same plant. The fact that somewhat similar heritable variations keep reappearing suggests chromosome aberrations, such as Blakeslee finds in *Datura*. If so, this would be the first case of irregular distribution of chromosomes resulting in commercially valuable new forms. It is to be hoped that further investigations will clear up this point.

Whatever may be the cause of the changes, the results from Egyptian and other kinds of cotton show that valuable variations are taking place. These can be separated out by single-plant selections, and when properly isolated and

protected from deterioration by the roguing out of all off-type and undesirable plants, they can be maintained. Fig. 189 shows the improvement made in long-staple Upland cotton by the development of the Meade variety

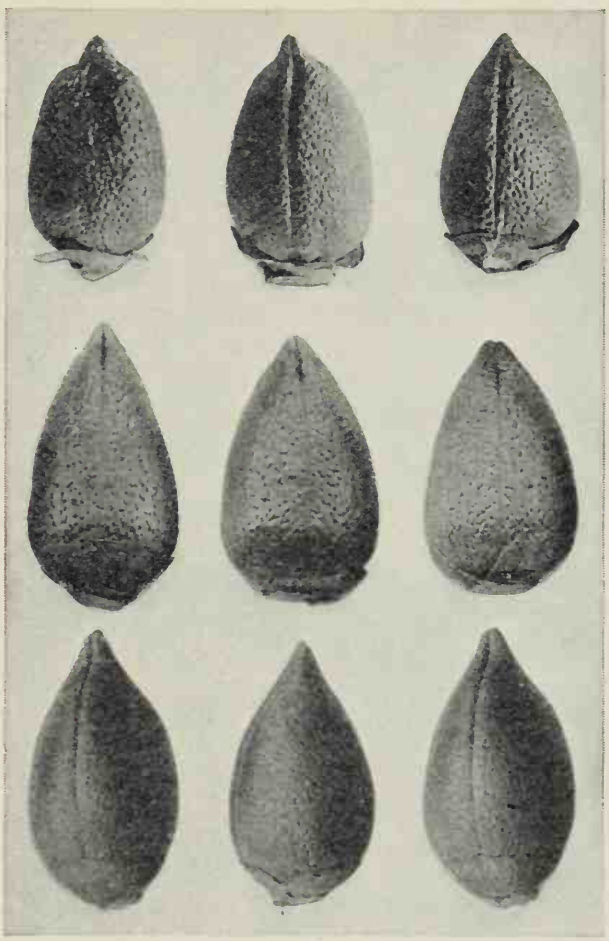


FIG. 188.—Characteristic differences in shape of boll and in surface markings of Mit Afifi (top), Yuma (center), and Pima (bottom) varieties of cotton. (After Kearney in Jour. Heredity.)

by the United States Department of Agriculture. The greater uniformity produced by selection is also apparent.

Naturally cross-fertilized plants.—The methods by which self-fertilized plants can be improved are simple and easily understood, as may be seen from the descriptions just given. In contrast to this, the normally cross-fertilized plants, particularly those propagated by seed, present dif-

ficulties which have not yet been satisfactorily overcome. The method of isolating single plants and proving their superiority by the progeny performance test is not adequate. As has been shown, organisms which have been in a constant state of hybridization are dependent upon the continuation

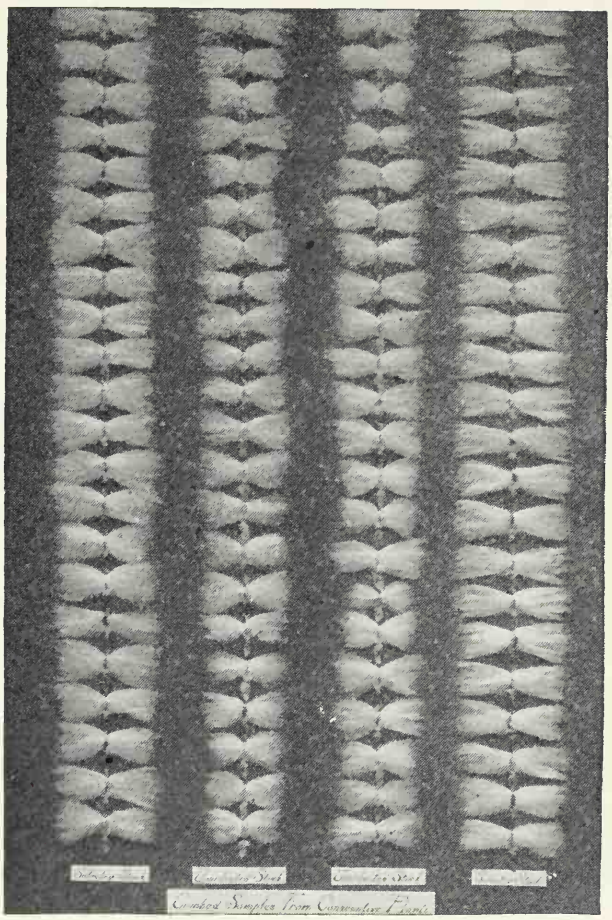


FIG. 189.—Cotton seeds with fiber, showing the effects of selection on the uniformity of Meade Cotton. The two center rows show combed lint from consecutive plants of the original unselected stock. Compare with the two outer rows from consecutive plants of the selected stock. (After Meloy and Doyle in U. S. Dept. Agr. Bull. 1030.)

of the same degree of heterozygosity in order to maintain vigor. Propagation from single plants reduces the amount of germinal diversity in the following generations and in nearly every case results in reduced vigor. Consequently, the lessened yield usually offsets any gain in other respects.

By selecting a large enough number of superior individuals and allowing them to interbreed, it is sometimes possible to maintain vigor; but the superiority of the selected cross-pollinated plants, as far as it has an hereditary basis, is practically always due to a chance combination of favorable factors. On account of segregation and regrouping of these hereditary factors, these desirable combinations are lost, with the result that the later generations as a whole may show little or no improvement over the average of the original stock.

Moreover, the selection of plants which approach the ideal sought for results in a tendency to bring together individuals of similar germinal composition, and even when large numbers of seed plants are used there is an appreciable reduction in heterozygosity, with its usual consequences. The more rigid the selection, particularly when uniformity is sought for, the more noticeable are the unfavorable results upon vigor and yield.

In spite of these handicaps, mass selection with cross-fertilized plants is successful in bringing about some improvement, especially in certain particular qualities, such as hardiness, early or late maturing, and disease-resisting characters which are not directly associated with reproductive ability. Sugar content, the size and color of flowers, the amount of stored food in the seed beyond the needs of the young seedling, all such characters are either not concerned with the plant's capacity to reproduce itself or are detrimental to it, and these can be appreciably altered by mass selection and sufficient vigor maintained at the same time.

Mass selection with sugar beets.—The first systematic attempt to increase the capacity of a plant in a particular direction was made with the sugar beet. This plant began to be used for sugar production in Europe during the first part of the nineteenth century. At first, selection for seed production was made upon no other basis than size, shape, and color of the roots, but attention was later paid to finding roots having a high percent of sugar. Louis de Vilmorin,

of the seed firm of Vilmorin, in Paris, having practiced mass selection with carrots and other vegetables, turned his attention to the sugar beet. Roots were tested for specific gravity by placing them in solutions of different density. This was a rough determination of the percent of sugar in the roots, since the sugar increased the relative weight of the roots. Later this method of analysis was superseded by taking a part of the root, without injuring its viability, extracting the juice from the sample, and measuring its comparative density. At first this was done by weighing a silver ingot suspended in the extracted juice. Later, the polariscope was used. Beets which showed a high percentage of sugar and had at the same time sufficient size and suitable shape, and were otherwise desirable, were used for seed production. This method has been continued on an extensive scale, and at present some of the seed growers in Europe analyze each year more than 300,000 individual beets in order to select their roots for seed production.

The first analyses available show that the beets used during the early period of sugar manufacture averaged about 6 percent of sugar. The accuracy of these first determinations is somewhat doubtful, as the methods of analysis were greatly improved in later years. The variation in sugar content among individual roots at that time is not known. In 1878, at the Paris Exposition, there were exhibited varieties which averaged from 16 to 18 percent, and individual specimens went as high as 25 to 28 percent. In the forty years that have elapsed since that time, continued selection has failed to make any appreciable progress.

If we grant that 6 percent represented the average sugar content at the beginning of the industry, the difference between that and 17 percent does not mean a proportional increase in sugar production per acre. It has been shown by other plants that increase in percentage of particular components is usually obtained only by some sacrifice in yield, and this probably has been true with sugar beets.

But even though this has been the case, there is no

doubt that an appreciable increase in sugar production per unit of area has been brought about and the plants better adapted to the particular purpose to which they are now put. The improvement was made early in the development of the industry, and selection now does no more than keep the plants at their high level of production. The increased sugar production has been accomplished by the elimination of the strains of low sugar content. There is no proof that the inherent capacity of the plant to produce sugar, as shown in individual specimens, has been greatly altered. In fact, it is quite likely that a few beets in the original unselected material may have analyzed just as high as any that are grown at the present time. There are now simply more of these high producers.

Possibilities of further increase in yield of sugar.—Any increase in percent of sugar or production of sugar per acre by a continuation of the method of mass selection is very unlikely. Pritchard has shown conclusively that the hereditary differences in sugar beets are difficult to detect on account of the great fluctuation due to environmental influences. He finds that beets of low analysis are now as productive as those high in sugar content, and that the commercial seed which is one generation removed from selected mother plants gives as high weight of beets and percent of sugar as the progeny direct from selected beets.

According to Pritchard, the extensive mass selections now made are not needed to maintain present production, and future improvement is to be looked for in a more careful progeny test of individual plants, carried out in such a way as to clearly distinguish between hereditary differences and mere fluctuations due to soil and accidental differences. To accomplish this, more attention must be paid to increasing the amount of seed per plant, in order to have enough plants upon which to base an accurate comparison. On account of the inconstancy of heterozygous combinations, which are in the majority in a cross-pollinated plant like the

sugar beet, it is doubtful if even careful progeny tests will result in any appreciable improvement unless the heredity is controlled through the pollen parent as well as through the seed parent.

Selection in the cross-fertilized corn plant.—For more positive information in regard to the effectiveness of selection with cross-fertilized plants, we must turn to maize. Since this crop is grown on a larger area than any other cultivated plant in this country, it is only natural that much effort should have been put forth to increase the productivity and usefulness of this crop for particular purposes.

The first extensive selection toward definite standards was carried out in the first half of the nineteenth century, in the production of Leaming, Reid's Yellow Dent, Boone County White, and other well-known varieties. From the first, attention has been paid principally to the characters of the ear rather than to those of the plant which produces it. Following the extensive development of the corn shows in the latter part of the past century, and the increasingly keen competition for prizes, certain standards were set up to facilitate judging. At first these were used to evaluate the excellence of a given crop of corn as grown, rather than as seed to be planted. It was but natural, however, to consider the prize-winning ears as the most desirable for seed. In time, elaborate specifications were arbitrarily propounded as the ideal toward which corn should be selected. These were embodied in the score card.

Ear characters emphasized by score card.—The qualities emphasized for exhibition purposes were generally followed in the selection of seed corn. Particular attention was paid to those features which increased the proportion of grain to cob, such as deep and compact kernels, well-filled butts and tips, cylindrical shape of ear with a diameter properly proportioned to cob to give the greatest percentage of shelled grain. It was taken for granted that a plant which produced an ear of this idealized type was more efficient in its growth and reproductive processes, and it was thought

that seed from such an ear would therefore tend to give somewhat higher yields than corn not so selected.

The practice of selecting seed on this basis, although widely preached, was not founded upon experimental proof. A large number of investigations have since shown clearly that many of the characters particularly emphasized on the older score cards are not associated with ability to yield and some are actually antagonistic, particularly in those regions outside of the most favorable corn-growing districts. The net result from these investigations has been to show that there is no universally best type of ear for all conditions or even for the same environment. Yield is determined by the ability of the plant to grow, rather than the form of the ear, and is more concerned with food assimilation and cell division than with external structural details.

Altering the chemical composition of corn.—In 1896, Hopkins, at the Illinois Station, began an experiment to alter the chemical composition of corn. Four series of selections were started and have been continued to the present time; these are high and low protein and high and low oil content. From a variety of dent corn known as Burr's White, a large number of ears of good size and form were analyzed. From these, several ears which deviated the most in the desired direction were taken, and each was planted in a row by itself. From the plants grown, the rows that gave the best average showing in the desired direction were selected to furnish seed for the next year's planting. In turn, the highest-analyzing ears were chosen, in each generation, from the progenies that were above the average.

In this way, selection was based upon the character of the crop grown, rather than the seed planted. A marked response in the direction of selection was obtained, as shown in Chapter IX. The change was most noticeable in the first period, but has continued up to the present time. The increase in chemical composition has been offset in part by a decrease in yield, although the total production of the

FIG. 190.—One of a very few cabbage plants remaining in a field practically destroyed by yellows. This single plant was the beginning of a resistant variety. (After Jones, Walker and Tisdale in Wisconsin, A. E. S. Research Bull. 48.)

particular ingredients sought for per acre has been increased, as shown by Smith.

Ear-to-row method of corn breeding.—This system of selection became known as the ear-to-row method of breeding and was widely applied to other characters of the corn plant and particularly to yield. It was found that such characters as height of plant, position of ear on the stalk, angle at which the ear is held when mature, and similar details of

FIG. 191.—The difference between disease-resistant seed and unselected seed of cabbage grown on land heavily infected with cabbage yellows. (After Jones, Walker and Tisdale in Wisconsin A. E. S. Research Bull. 48.)

the plant's structure could be more effectively altered in this way than by simple mass selection. In regard to yield, however, the results are conflicting, and the consensus of opinion, as recently summarized by Richey and by Kiesselbach, is that very little actual increase in production can be brought about in this way and permanently maintained.

Disease-resistant cabbage.—The principal value of selection with cross-fertilized plants, without controlled pollina-

tion, is in adapting varieties to new regions or altering them for special purposes. Marked success has been obtained by L. R. Jones, at the Wisconsin Station, in selecting disease-resistant strains of cabbage, a partly cross-fertilized plant. A few surviving plants were found in fields that were almost completely killed out by disease. These were isolated for several seasons, until the resistant qualities seemed to be fixed. Then a number of these single-plant strains were combined and carried on by mass selection. The plants used for seed purposes are being grown on soil known to be heavily infected, in order to prove the continuation of their resistant qualities.

Lack of control over the heredity in cross-fertilized organisms.—The difficulty in working with cross-fertilized plants is the inability to control the heredity through the pollen parent. Selection based upon the qualities of the seed parent is of little avail, as long as the pollen comes at random from plants good, bad, and indifferent. The heterozygosity maintained in this way makes it impossible for the plants to breed true to the characters for which they have been selected, unless these characters are relatively simple in their inheritance.

The situation would be the same in animal breeding if selection were confined solely to the qualities of the dams and no attention whatever paid to the sires. Theoretically, the pedigree record system used in animal breeding could be applied directly to plants. Some individuals could be selected as seed parents and others as pollen parents. Pollination could then be carried out by hand. This practice, continued from generation to generation, would undoubtedly afford as much control over the heredity in plants as it has afforded in animals.

However, such a system is wholly impracticable for the reason that plants are individually of too little value and are so short-lived that the expense would be prohibitive. Moreover, with corn and many other plants, the character with which selection is chiefly concerned, seed production,

is not visible until after the time for pollination. There is need, therefore, of a radically new procedure which will permit a more complete control of the heredity through both sexes and at the same time avoid the disastrous effects of inbreeding.

Selection in self-fertilized lines.—Self-fertilization, as has been repeatedly shown, automatically sorts out a heterozygous complex into an almost infinite number of fixed, true-breeding strains. Many serious abnormalities, forms of sterility, and weaknesses are quickly eliminated. This in itself is a real gain. But the greatest opportunity

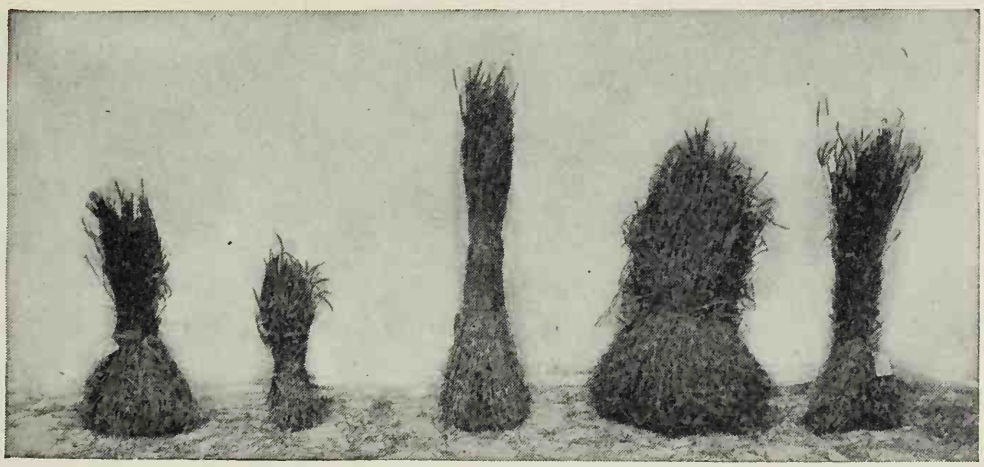


FIG. 192.—Diverse types of timothy obtained from single plant selections. The problem in a cross-fertilized species like timothy is to hold desirable types after they are found. (After Webber in New York (Cornell) A. E. S. Bull. 313.)

that inbreeding makes possible is in the ability to select for the best heredity during the reduction process. Selection in self-fertilized lines from a heterozygous stock, up to the time that homozygosity is attained, makes possible the only thorough means of obtaining the best that there is in a crossbred race. It is to be expected that most of the strains resulting from inbreeding will have only medium value. The bulk of the germplasm in any crossbred material is mediocre. But the opportunity is there to select for the very best that is in the material started with, unhampered

by the masking effect of hybrid vigor. Particular qualities can be brought out with a certainty never before realized in crossbred plants. The results from self-fertilized lines carried on in this way will depend, of course, upon how extensively and skillfully the selection is carried out. There will be a few strains which are potentially superior to all the others. The difficulty is to recognize these, as their

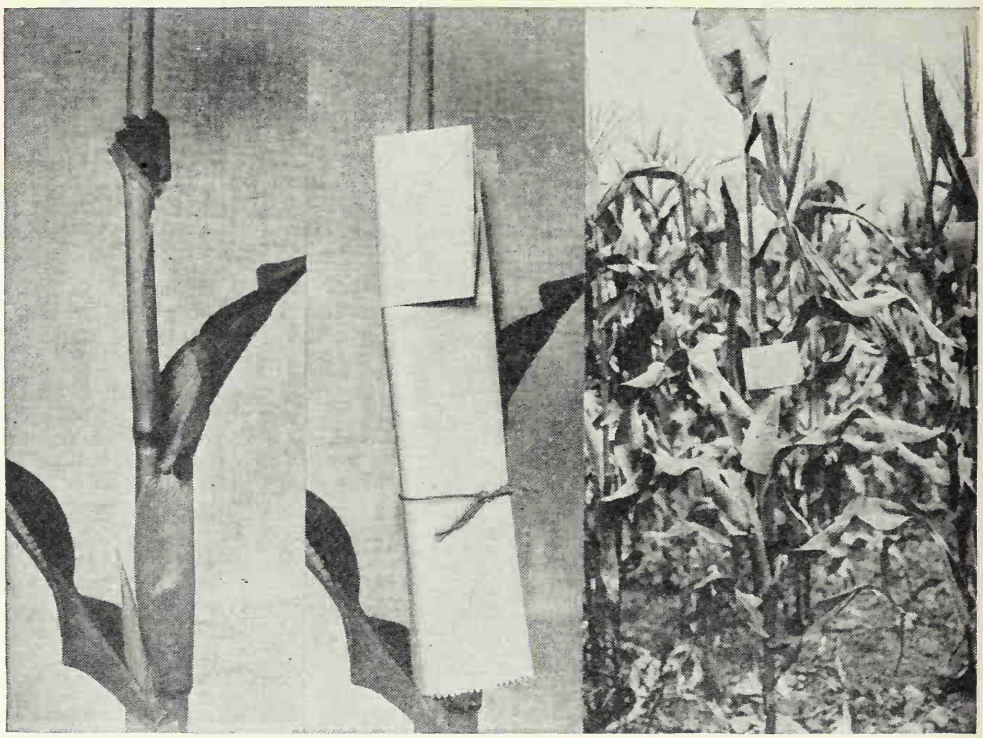


FIG. 193.—Hand-pollinating corn. Ear shoot before silks appear, ready to bag; ear shoot enclosed in a paper bag; and a plant with both ear and tassel bagged.

good qualities are often not clearly brought out until they are combined with other strains.

Methods of utilizing inbred strains.—The best methods of utilizing inbred strains have not yet been fully worked out for different crops, but there are several ways which are theoretically possible and seem entirely practicable.

1. It is possible to obtain inbred strains which are not reduced below the vigor of the original stock and may even be increased in this respect. The chance of obtaining this

result is so remote that it is not likely to be an important means of improvement; but the possibility is there, and such homozygous forms, when once obtained, would have great value because of their uniform growth and even production from every plant. They would be exactly like naturally self-fertilized plants and would be as easily propagated,

FIG. 194.—Hand-pollinating corn. Gathering and applying pollen. The silks are cut back to about 2 inches above the tip of the ear with a knife sterilized in alcohol, care being taken to avoid touching the silks with the hands in order to prevent contamination with undesired pollen.

although greater precaution would have to be taken to prevent out-crossing.

2. Inbred strains can be crossed and only the first generation used for production purposes. This is practicable only with plants propagated by seed, which can be easily crossed. Since the first generation of a cross between fixed types is as uniform as the parents, the even production from every plant holds out the possibility of a marked improvement. The use of first-generation hybrids may be carried

further by combining more than two strains by successive crosses, as will be explained later.

3. A sufficient number of inbred strains possessing the qualities desired can be combined. In this way a new variety can be re-created out of the purified and selected survivors of a crossbred race and maintained by open-pollination in the same way as before being inbred. Such a variety would be somewhat variable and would have to be continually selected in order to be maintained at a high level. This method of breaking up, purifying, and synthesizing is applicable to all kinds of cross-fertilized plants.

Selection in self-fertilized lines applied to corn.—The application of selection in self-fertilized lines is best illustrated with corn. Starting with one or more varieties which are known to be adapted to the conditions under which the corn is to be grown, the best appearing plants are artificially self-fertilized. At maturity the hand-pollinated ears of good size and type, which have been produced on plants that have come through the season in good condition, are selected.

Each of these ears, self-fertilized for the first time, is the starting point for an inbred line. They are planted separately in rows the following year, and the best plants are again chosen for seed production. Several progenies in each line, from self-fertilized ears, may be grown in the second year and compared in the field at pollinating time, but only the best progeny in each line is selected as the progenitor of the next generation. The importance of basing selection upon the progeny in this way is easily understood when it is noted that the best-appearing hand-pollinated ears do not always give the best plants in the following generation. This procedure, which is illustrated diagrammatically in Fig. 195, is continued until a reasonable degree of uniformity and constancy is attained.

The number of self-fertilized lines to be carried along depends upon the facilities available. The number of plants to be grown, the number of hand pollinations to be made,

and the number of progenies to be compared depend largely upon the character of the material. It is important to start with as large an amount of different material as possible. For this reason it is better to grow a large number of self-fertilized lines than to give the same amount of effort to making many selections within a few lines. It is more important to grow numerous progenies, having relatively

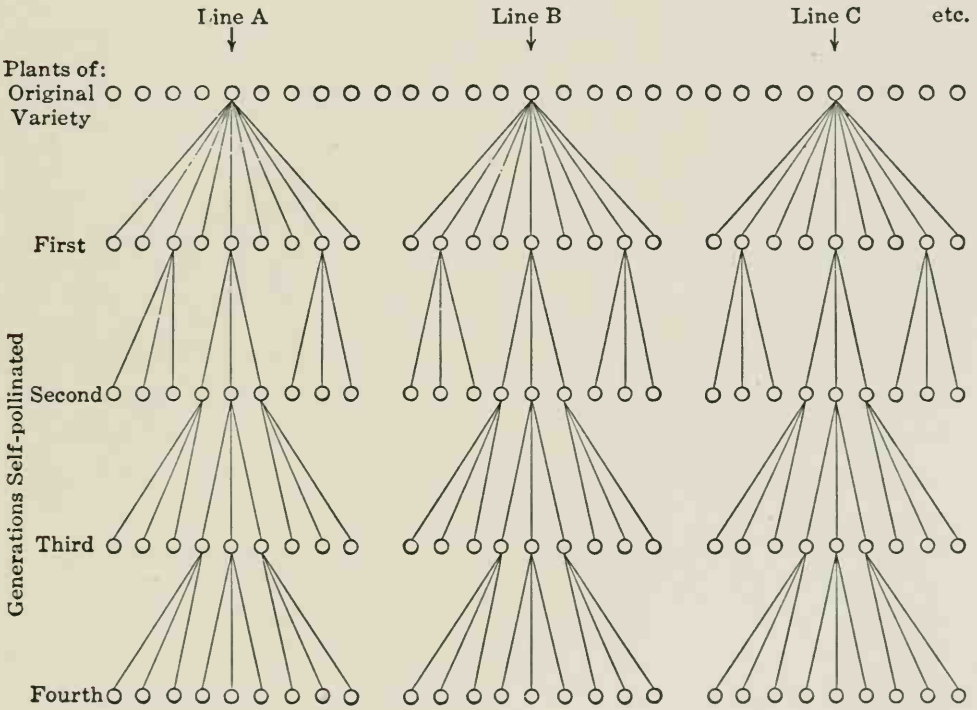


FIG. 195.—Diagram showing a method of carrying on selection in self-fertilized lines. A number of individual plants are self-fertilized and each becomes the starting point for an inbred line. From the progeny of each, certain plants are again self-fertilized and their progenies grown, but only one is chosen to continue the line.

few plants in each if necessary, than to grow large numbers in a few progenies. This is because it is difficult and often impossible to recognize desirable plants at pollinating time. The value of a selection becomes clearly apparent only after its offspring are grown and compared with other progenies.

Every effort should be made to insure that desirable, high-yielding strains are included at the start. There is, however, no very close correlation between the appearance

or performance of the plants used at the start and the inbred strains which finally result from them. Excellent self-fertilized families may be secured from very unpromising ears, and many fine specimens grown in the open field will become worthless when inbred.

Selections should take into consideration the uniformity of the progeny as much as yield and vigor of the plants.

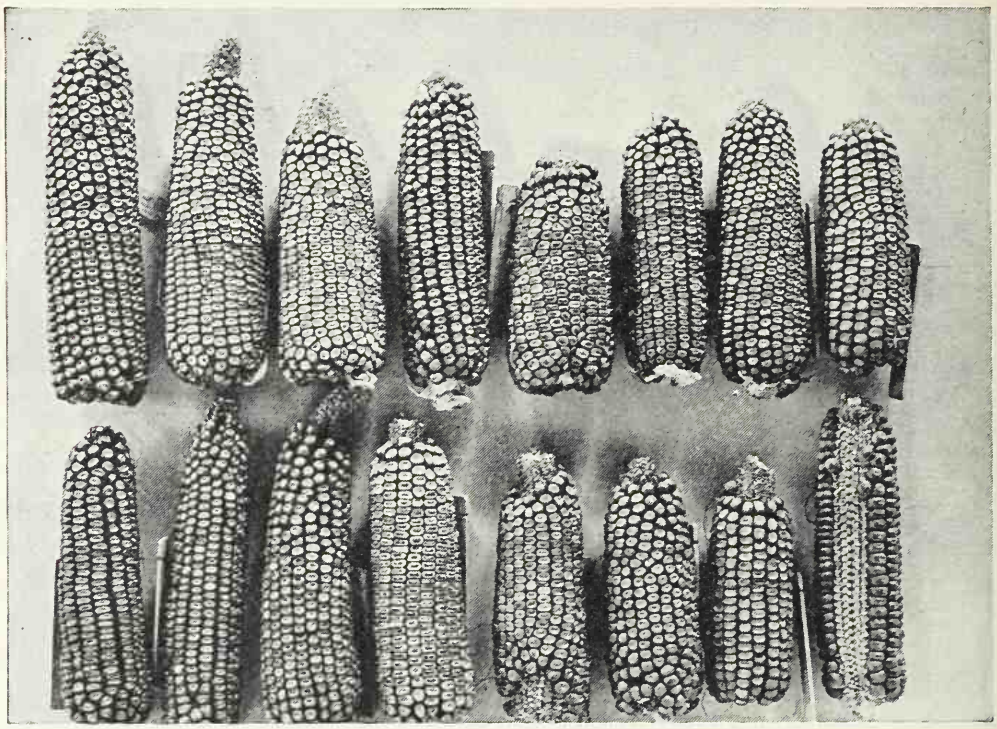


FIG. 196.—Hand-pollinated ears grown on selected plants, each of which is the beginning of a self-fertilized line. In the top row they are numbered 1 to 8 (left to right), bottom row 9 to 16.

High yield and exceptional vigor in variable lines means that the plants are still heterozygous and their good qualities may be lost when uniformity is finally secured. The aim is to have the best hereditary factors reduced to a sufficiently homozygous condition to insure the permanence of their good qualities. This is not a simple matter, and the best methods of selection in self-fertilized lines have not yet been completely worked out.

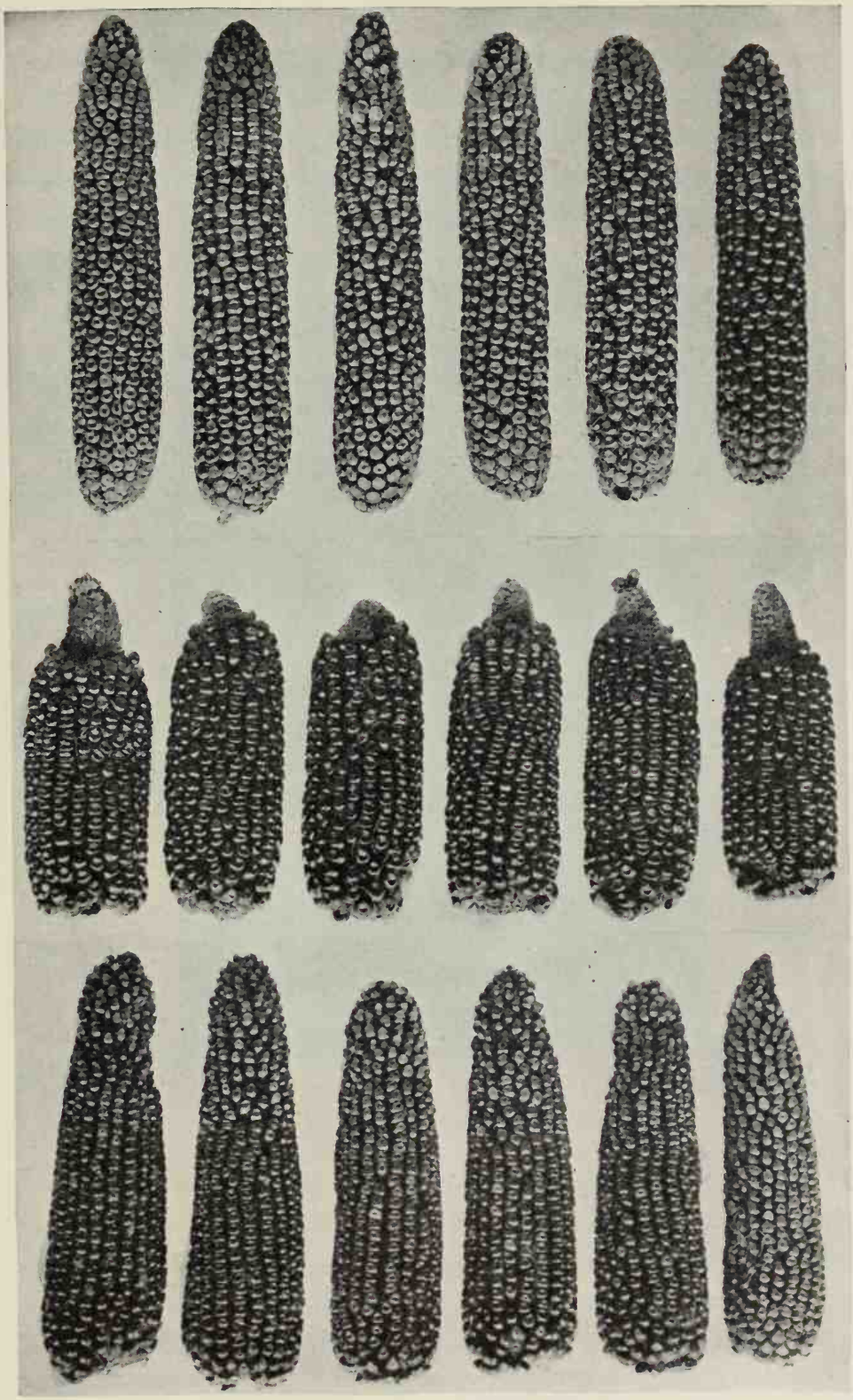


FIG. 197.—Inbred strains after four generations of self-fertilization. From top to bottom they are from ears numbered 1, 4, and 6 shown in Fig. 196.

Diversity of inbred lines.—After a few generations of self-fertilization, very striking differences are shown in the different lines. Many abnormal characters appear and are quickly eliminated. Rigid adherence to self-fertilization in every case insures that all forms of sterility are gotten out and only the strongest plants survive. All lines which

FIG. 198.—Two self-fertilized lines of corn, showing a marked difference in ability to stand up in the field.

do not produce a reasonable amount of seed and all strains which show serious weakness and any outstanding undesirable characters should be discarded. The remaining selfed lines will differ greatly in productiveness.

Possibility of obtaining inbred corn not reduced in vigor.—As yet, no uniform strains have been secured which equal in vigor or yield the crossbred stock from which they

came. Theoretically, if all the favorable dominant factors were brought together in the homozygous condition in one individual, that plant and its descendants should be even more productive. As brought out in Chapter XII, this follows from the fact that dominance is seldom perfect and a double dose is usually somewhat more effective than a single dose of most factors.

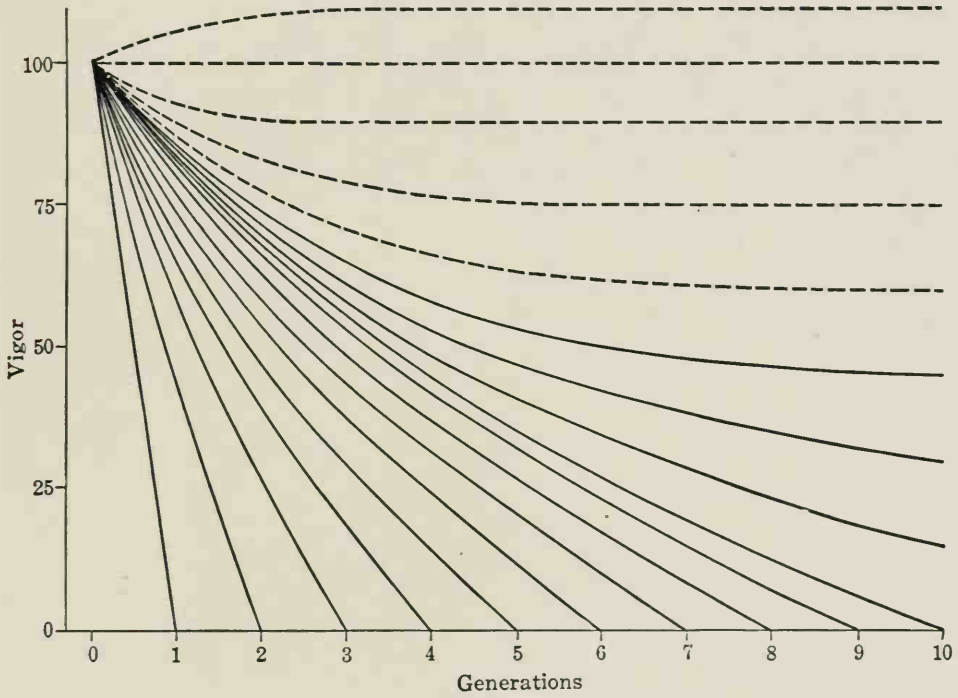


FIG. 199.—Diagram showing the actual and theoretical results of self-fertilizing corn. The solid lines represent strains already obtained which have either become extinct or have been reduced to 50 percent or less of the vigor of the original variety. The broken lines represent strains which can be expected theoretically when this plant is worked with more extensively.

Importance of obtaining vigorous inbred strains.—While it is true that many unpromising inbred strains have potentially high value and do exceptionally well when crossed in suitable combinations, their poor growth makes them difficult to work with, and in general they should be discarded as soon as possible. Although there are many exceptions, the best inbred strains will usually give the best results when crossed.

Some promising strains in a fairly uniform and stabilized condition can be obtained and recognized after three generations of self-fertilization. Most of the good strains can be positively identified in the fourth. Nearly all of these will show some further reduction in size and vigor up to the sixth generation and even beyond, but for practical purposes

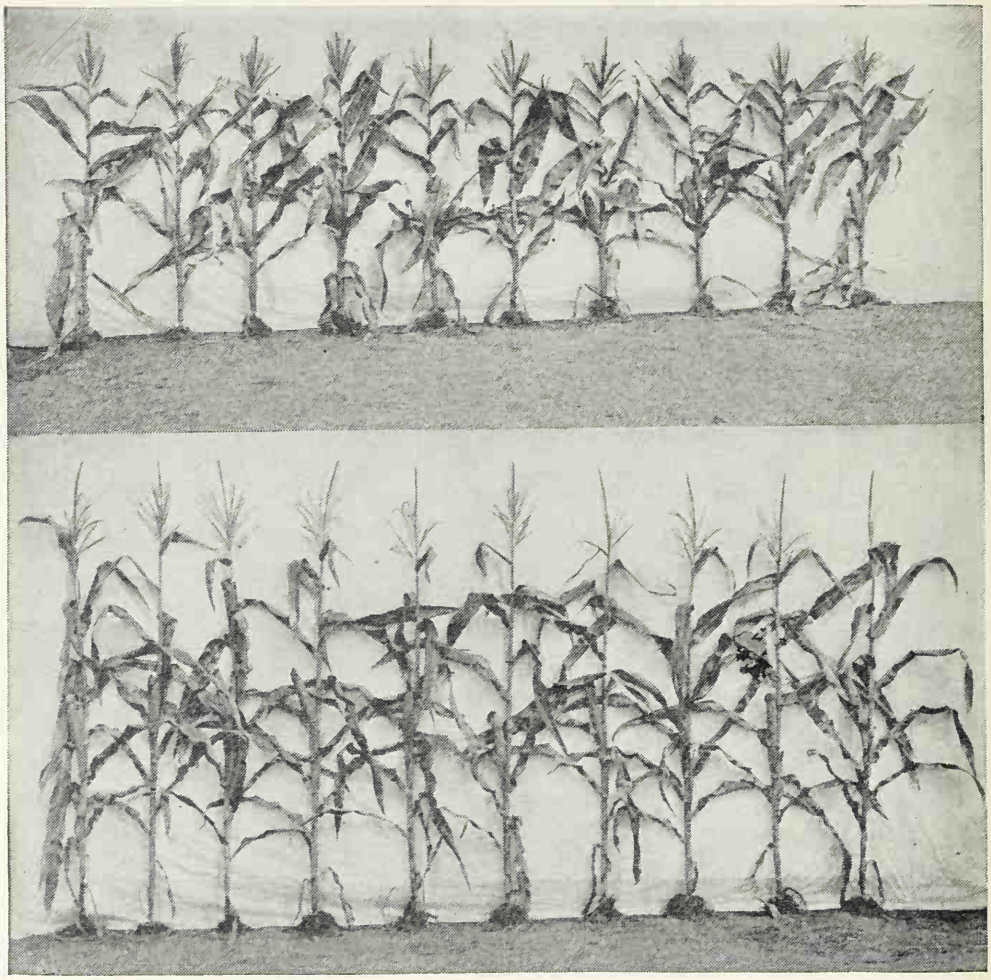


FIG. 200.—Two self-fertilized strains of corn, showing evenness in height and uniformity in structural details.

it has been found that three or four years of self-fertilization is sufficient to obtain good material. Approaching homozygosity can be recognized by evenness in height of plant and uniformity in minor structural details.

Testing inbred strains.—The inbred strains finally selected have to be tested in all possible combinations. For

practical purposes it may be assumed that reciprocal crosses give the same results. This is not always true, however. Crossing can be carried out by hand pollination or by planting all the strains in one isolated block and detasseling all but the one to be used as a pollinator. Care must be taken to plant the pollinators at different intervals

FIG. 201.—Differences obtained in self-fertilized lines in four years, selected for vigor of plant and yield of grain but not for height.

and in sufficient quantity to provide pollen for all. Only a few detasseled plants are needed to supply sufficient seed to test. With several such crossing plots, all the combinations can be tested in time.

Value of first-generation hybrids between inbred strains.—The first-generation crossed plants are often remarkable

for their vigorous growth, even flowering and maturing, and uniform production of grain. In the latter lies the greatest possibility of securing high yields. If the parental strains are homozygous, all the first-crossed plants will be alike to a degree which is astonishing in comparison with the inter-pollinated varieties of corn commonly grown. A valuable combination, when once secured, can always be had every time that particular cross is made. In other words, the

FIG. 202.—First-generation hybrid of two inbred strains of corn.

good results can be had indefinitely as long as the stock strains are kept pure.

Hybrid seed production not limited to one locality.—Furthermore, the crossbred seed need not be produced in the region in which the hybrid plants are to be grown. The seed can be raised almost anywhere, as long as the grains are properly grown and ripened so as to furnish good germination and seedling growth. Since the inbred strains are fixed, they will not change their adaptability for one region by being grown in another, except possibly after long

periods of time. A combination which has been found to be desirable in one locality, for example, central Illinois, can be grown from seed produced in California or Pennsylvania, if this were desirable, without danger of changing the adaptability of the hybrid to the particular conditions of central Illinois.

A change of climate and soil apparently has some direct

FIG. 203.—Some of the same plants shown in Fig. 202 with husks and leaves removed.

immediate effect upon corn and many other plants as well, irrespective of adaptation. Collins calls this "new-place effect" and has shown that with corn it tends to increase productiveness somewhat. Seed grown in California, Illinois, or Pennsylvania may behave slightly differently when grown in Illinois, but the important point is that when the result from one locality is once known after adequate test-

ing, that result can be expected thereafter. Actual results show that hybrid seed from the same parental stocks produced in Iowa and Connecticut give practically equal results when grown together either in Iowa or Connecticut.

Crosses between inbred strains handicapped.—The first cross of inbred strains of corn is handicapped in several important ways. The inbred plants, for the most part, are unproductive as compared to normal corn. Therefore the hybrid seed is expensive to produce. The seeds are small and poorly stored with food and the plants produced from them start more slowly and are smaller than plants from

FIG. 204.—The same plants shown in Fig. 203. Note the uniformity in size, shape, and type of ear. With one exception, all ears in this lot are placed at the sixth node.

large seeds. It takes them several weeks to catch up with the more vigorous seedlings, and under unfavorable conditions this is a drawback that the hybrids are unable to overcome. It is possible that inbred strains will be obtained which are very little if at all reduced in size of seed and vigor of the crossed seedlings grown from them, and crosses with such plants as the seed parent would not be handicapped in this way.

Disadvantage of uniformity.—The extreme uniformity in size of growth and time of flowering and maturing, characteristic of the hybrids between two fixed strains, may in itself be disadvantageous in that the plants may

all be affected adversely by unfavorable weather at a critical time and for that reason may not do as well as a more variable variety which would be more adaptable. Zavitz, at the Ontario Station, has shown that combinations of different kinds of small grains, such as barley and oats, yield more than the average of either grain grown separately. He failed to find, however, that mixtures of different varieties of the same grain gave any increase in yield except to a small extent in the case of barley. Corn at pollinating time is more subject to weather injury than most crops, and it may be that some variability in time of flowering is desirable.

Double-crossed corn.—All of the above considerations make it worth while to carry the crossing one step further. Two first-generation hybrids are again combined to produce what has been called a double cross to distinguish it from the single cross of two inbred strains. In this way four different self-fertilized lines are brought together as follows:

Inbred strains	A	B	C	D
Single crosses	A×B		C×D	
Double cross	(A×B)×(C×D)			

It is essential that the four strains be of such composition that the single crosses made from them, in all six possible combinations, AB, AC, AD, BC, BD, CD, are all equally vigorous and productive. Even this does not make certain the value of the double cross, and the result may be different according to the way in which the four strains are put together. It is necessary to establish the value of any particular combination by trial, but when once produced it can always be reproduced.

Since the single-crossed plants are forming segregating gametes, the double-cross will be composed of plants which are all unlike in some respects. But, as the combinations will be heterozygous in practically every case, recombination can not take place in such a way as to allow recessive

weaknesses to appear. Theoretically, the plants will be no less vigorous than the first cross, and since the plants of the double cross come from large, well-nourished seeds they should be somewhat more productive on account of their better start. This has been shown to be the result in a

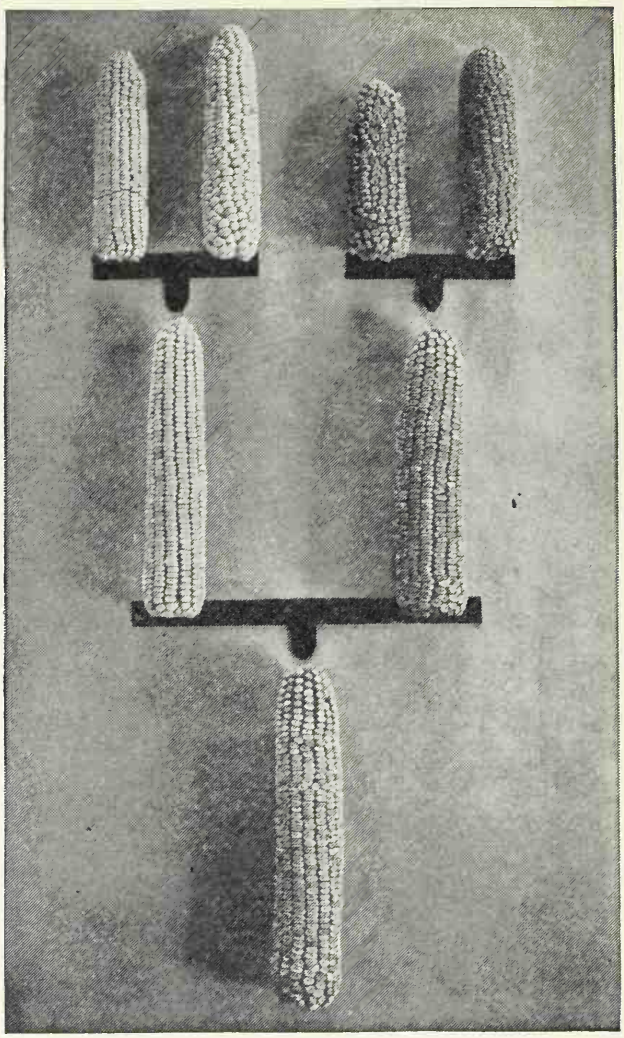


FIG. 205.—Diagram showing the method of double-crossing corn in which four inbred strains are combined by three crossings.

large series of comparisons made at the Connecticut Station; and while the double-crossed plants differ from each other in minor details and vary somewhat in time of flowering and ripening, they are all essentially first-generation hybrids and when grown under favorable conditions show the

uniform production of even-sized and well-developed ears from every plant, barring accidents, characteristic of first-generation hybrids between two homozygous strains.

Corn hybrids do not maintain high yield.—Like the single crosses, the quadruple combination will not maintain its full vigor in the following generations, and will fall off in yield from 15 to 20 percent on the average, as has been shown by test. This reduction takes place whether the seed comes from inbred plants or from naturally intercrossed plants selected as the best from large numbers. In the latter case the reduction is not so great, but it has

FIG. 206.—Two single crosses (outside) and their reciprocal double crosses (inside), showing the comparative yield of the four types.

been clearly shown that the later generations will not give as good results as the first crossed seed.

This means that, to gain the maximum value of inbreeding, crossed seed must be planted each year. Seed produced in this way costs appreciably more than seed corn as now produced. It takes considerable time to develop a combination suitable for any one locality, and the area in which that particular cross can be successfully grown is more or less limited.

Maintaining inbred stocks.—After the self-fertilized strains are reduced to homozygosity, it makes no difference whether they are self-fertilized or intercrossed, since the plants of one line are all exactly alike. Therefore, hand

pollination is no longer necessary. The plants can be crossed by planting two kinds in alternating rows in one field and detasseling all the plants of one kind. In this way, crossed seed is obtained from the detasseled plants and inbred seed from the pollen-producing plants. This pure seed can be used for planting again in the crossing plot. By alternating the pollen parent each year, and making the cross both ways, it is possible to produce crossed seed continually and maintain the stock seed.

Development of crossbreeding methods.—This method of producing crossed seed was first advocated by Beal at the Michigan Station, in 1878, and again by McCluer, in 1892, at the Illinois Station. The method of inbreeding and then crossing was developed independently by G. H. Shull of the Carnegie Institution and East at the Connecticut Station, and the preliminary results published in 1908. The full importance of selecting during the inbreeding was not realized until the conception of hybrid vigor as due to dominance was developed. The best results from crossing are only obtained where there is the best potential heredity in the material crossed.

Controlling heredity and maintaining vigor.—In order to control the heredity in naturally cross-fertilized plants, so that the type can be held constant and factors for barrenness, weakness, and susceptibility to disease kept out, a certain degree of homozygosity must be maintained. In corn this has always tended to reduce maximum vigor. All the evidence shows that it will be easier to secure the largest yields, together with the greatest assurance of maintaining those yields and retaining the type unchanged, by some system of crossing. Although the best method remains to be worked out, it now seems certain that any marked improvement in corn must be based upon inbreeding followed by crossing.

Selection in self-fertilized lines applied to other crops.—Selection in self-fertilized lines, which has been outlined in considerable detail in its application to corn, is available

for use with all other naturally cross-pollinated plants. However, the utilization of first-generation hybrids is strictly limited. The cucurbits can be treated in this way, because the plants are monoecious and the flowers can be easily distinguished and the staminate flowers removed before they open, provided the growth of vine is kept pruned back. Since these plants are insect-pollinated, different plots can be isolated by screening and hand-pollinated until suitable strains for crossing are developed. Probably neither squashes nor pumpkins are of sufficient value to justify this expense. Cantaloupes, watermelons, and cucumbers for pickling and growing in the greenhouse have considerable commercial importance.

Utilizing first-generation hybrids.—The long life and high individual value of certain shade, timber, and nut trees, which can not be satisfactorily propagated by cuttings, should justify investigation with a view to utilizing the vigor and uniformity of first-generation hybrids.

Tomatoes are easily crossed and produce enough seed from each pollination to make the production of first-generation hybrid seed feasible. Wellington at the New York Station, and Hayes and Jones at the Connecticut Station have found that some varietal crosses give an average of 15 percent greater yield, as well as an increase in earliness of ripening. This would justify the use of hand-pollinated seed, particularly in the greenhouse and for an early market crop.

Numerous tests have shown that some corn-variety crosses, without previous selection, are sufficiently more productive than either parent to make the planting of crossed seed each year profitable. This is particularly true in northern regions where early maturity is of prime importance. Crosses of dent and flint corn in New England, and dent and flour corn in the northern plains area have, on the whole, given the best results. Combinations of the dent varieties commonly grown in the Corn Belt have little or no advantage over the best varieties grown there. However,

a cross of dent grown in Iowa with flint from Argentina has been found by Wallace to be high-yielding and early-maturing. Griffee has summarized the results from tests carried out in all parts of the country and shows that in 10 out of 16 experiments the average yield of the crosses was above that of the higher-yielding parent.

Variety crosses in cross-fertilized plants are as variable

FIG. 207.—First-generation hybrid between two varieties of tomatoes which in three years' trials gave an average increase of 15 percent in yield over the more productive parent.

and unstable as the varieties from which they are made and have the same disadvantages. If the expense of producing crossed seed is justified, it is worth the additional effort to make the crosses with fixed inbred strains or combinations of inbred strains which have been systematically selected in self-fertilized lines.

Heterozygosity of vegetatively propagated plants.—The same advantages that can be secured in seed plants by utilizing first-generation hybrids are easily obtained in plants reproducing vegetatively. Since Mendelian recombination is not possible without reproduction by seed, any individual which possesses a particularly favorable associa-

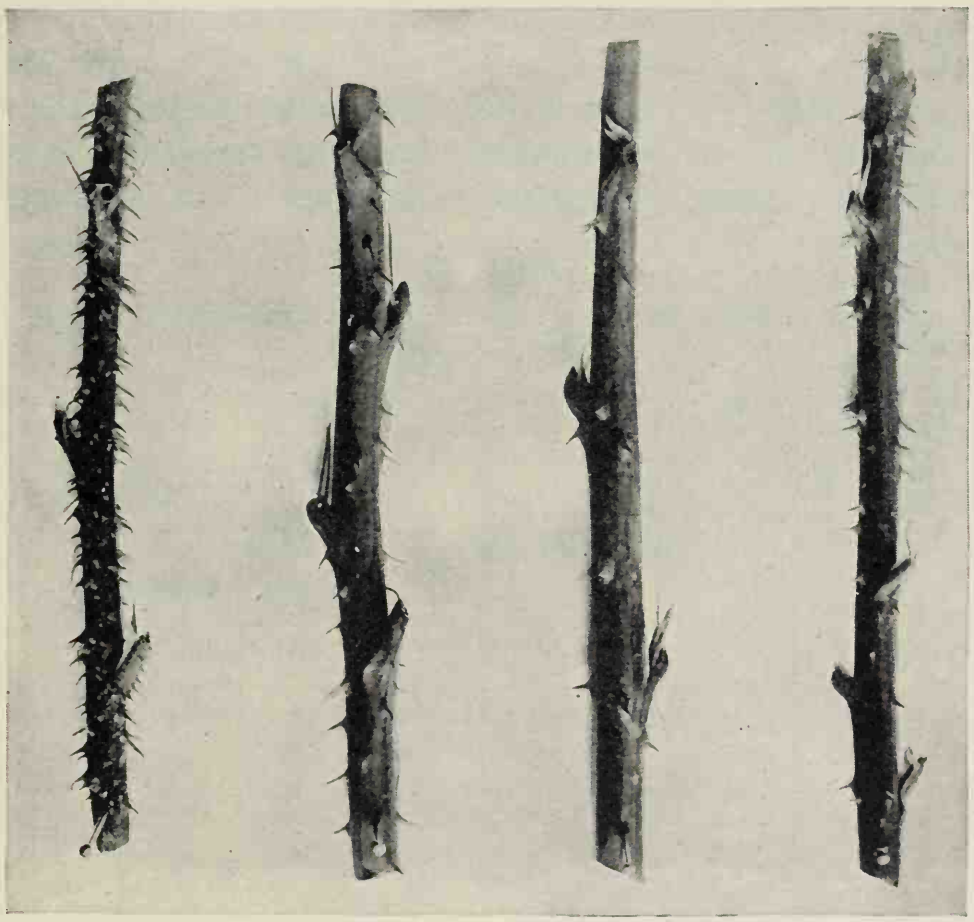


FIG. 208.—Variation in seedling raspberries in the number of spines. (After Anthony and Hedrick in New York (Geneva) A. E. S. Bull. 417.)

tion of characters can be multiplied without limit and, barring the rare occurrence of bud mutation or chromosome aberrations, will always come true to that type. Many varieties of apples have been grown for several hundred years without appreciable change in type. In Sweden, according to Newman, certain varieties of potatoes, known

to have originated over a hundred years ago, are still grown and are among the most valuable varieties. It is stated that the currant grapes grown along the eastern shore of the Mediterranean are the same varieties that were grown in the time of the Romans.

With vegetative propagation it makes no difference, as far as the uniformity of the variety is concerned, whether the plants are heterozygous or homozygous. Practically all plants that are propagated asexually are notoriously variable when grown from seed, and the seedlings in nearly every case are markedly less desirable than the variety from which they came, whether they are the result of self-pollina-

TABLE XLII

VARIATIONS IN COLOR OF FRUIT AMONG SEEDLINGS FROM SELF-FERTILIZED VARIETIES OF GRAPES

Data from Hedrick and Anthony, in New York, Geneva, A. E. S. Bull. 45

Parental Variety		Self-fertilized Seedlings			
Name of Variety	Color	Black	Purple to Dark Red	Medium to Light Red	White
Agawam	Purple red	1	2	..	2
Brighton	Dark red	6	5	9	7
Catawba	Purple red	2	4	3	4
Champion	Black	13	1	1	2
Clinton	Black	15	..	..	7
Concord	Black	40	6	..	12
Essex	Purple black to black	4	2	3	..
Hartford	Black	4	..	1	3
Hercules	Black	3	1	1	10
Isabella	Black	8	..	..	1
Merrimac	Black	9	3	6	..
Nectar	Black	4	5	2	..
Ozark	Black	16	..	..	..
Pearl	White	..	..	..	15
Regal	Dark red	..	..	15	5
Worden	Black	4	3	..	1
Wyoming	Dark red	1	4	2	3

tion or crossing with other varieties. This is positive evidence that plants which are reproduced otherwise than by seed owe much of their productiveness to hybrid vigor.

Self-fertilized apples, grapes, and raspberries.—At the New York (Geneva) Station, Hedrick, Wellington, and Anthony have found self-fertilized apple and grape seedlings to be regularly less vigorous than the crossbred seedlings. Apple seedlings from crosses of the same parental varieties differed in color of skin and flesh, shape, size, and texture of fruit. Some were sweet and some were sour. Grape seedlings resulting from self-pollination or known cross-pollination varied widely in color, shape, and quality of fruit. Crosses between two varieties of poor quality gave about the same result as crosses between two varieties of the best quality. It was noted particularly that many of the best commercial varieties failed to transmit their desirable qualities to their seedlings. Similar studies carried out with raspberries gave the same results. Variations in color and shape of fruit, spininess, and habit of growth of the plant were found in seedlings from the commonly grown varieties of this fruit.

TABLE XLIII

VARIATION IN COLOR OF TUBERS AMONG SEEDLINGS FROM CROSS-FERTILIZED POTATO VARIETIES

Data from Stuart, in U. S. D. A. Professional Bull. 195

Parentage of Crosses	Number of Seedlings								Percent	
	Total	White to Cream Yellow	Russet	Mottled	Flesh	Red	Purple	Violet to Black	Without Color	With Color
Irish Cobbler × McCormick	32	16	.....	2	11	3	.....	.....	50	50
Irish Cobbler × Irish Seedling	1425	982	18	36	229	104	55	1	70	30
Irish Cobbler × Keeper	870	589	17	23	141	98	2	.....	70	30
Irish Cobbler × Wild Chilean	214	73	.....	72	38	8	12	11	34	66
Extra Early Eureka × Keeper	680	480	.....	91	67	37	5	.....	71	29
Green Mountain × Keeper	88	69	1	11	6	1	.....	.....	80	20
Gold Coin × Keeper	322	257	.....	28	32	5	.....	.....	80	20
McCormick × Chilean Seedling	8	3	.....	4	1	....	.....	.....	38	62

Potato seedlings.—Stuart has made many crosses between potato varieties. The seedlings differed in color of tubers, as shown in Table XLIII. They also varied in size, shape, and other tuber characters, and equally as much in foliage growth.

This all goes to prove that vegetatively propagated plants are complex hybrids resulting from repeated crossing. All asexually reproducing plants that can still produce seed offer possibilities for new and better combinations of the characters already in existence. Most of the lead-

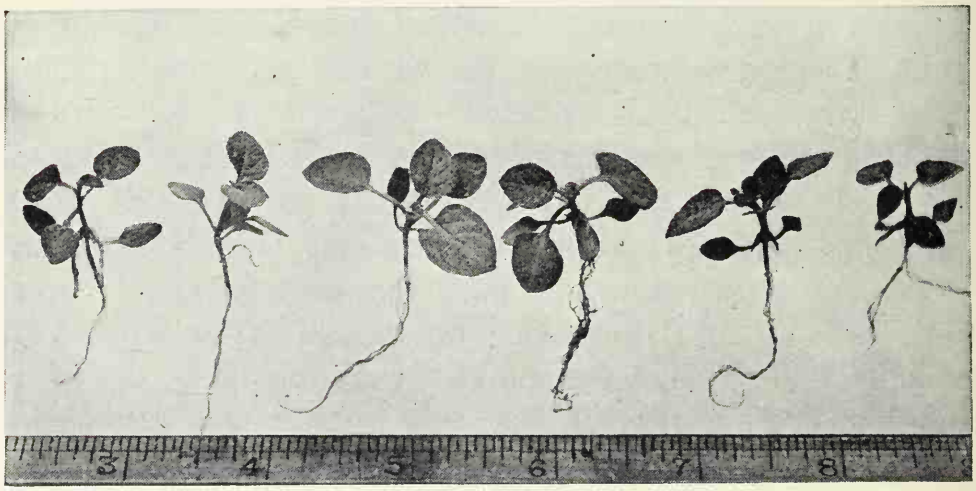


FIG. 209.—Young potato plants grown from seed. (After Stuart in U. S. Dept. Agr. Professional Bull. 195.)

ing varieties of apples, peaches, plums, cherries, blackberries, and raspberries have resulted from chance seedlings.

Origin of varieties of the apple.—Nearly 700 varieties of apples are listed by Beach in his "Apples of New York." Both parents are known for only one of these. Two have one parent known and the other guessed, and the seed parent only is given for 39 kinds. Of the remaining 650 varieties, 71 are known to be seedlings but of entirely unrecorded parentage. Only 4 are considered to have originated by bud variation, and these differ but little from the varieties from which they came.

Proportion of meritorious seedlings.—Out of 106 apple crosses which have fruited among 148 seedlings grown at the Geneva, New York, Station, 14 have been considered sufficiently promising to justify further trial. From 1898 to 1903, grape seedlings to the number of 1500 have been tested, and only 5 merit naming in the estimation of their originators.

Plants that mature quickly have been extensively

FIG. 210.—Differences in foliage shown by potato seedlings. (After Stuart in U. S. Dept. Agr. Professional Bull. 195.)

hybridized by controlled pollination. Strawberries, potatoes, dahlias, carnations, irises, tulips, gladioli, for example, have been notably improved by systematic crossing and selecting. The varieties that have been produced in this way and find lasting favor are for the most part merely chance combinations, winning numbers in a living lottery. For every individual of promise, thousands of plants must be grown and destroyed. All vegetatively propagated varieties, after countless generations of crossing and recrossing,

are genetically so complex that attempting to obtain further improvement by repeated crossing is like solving a

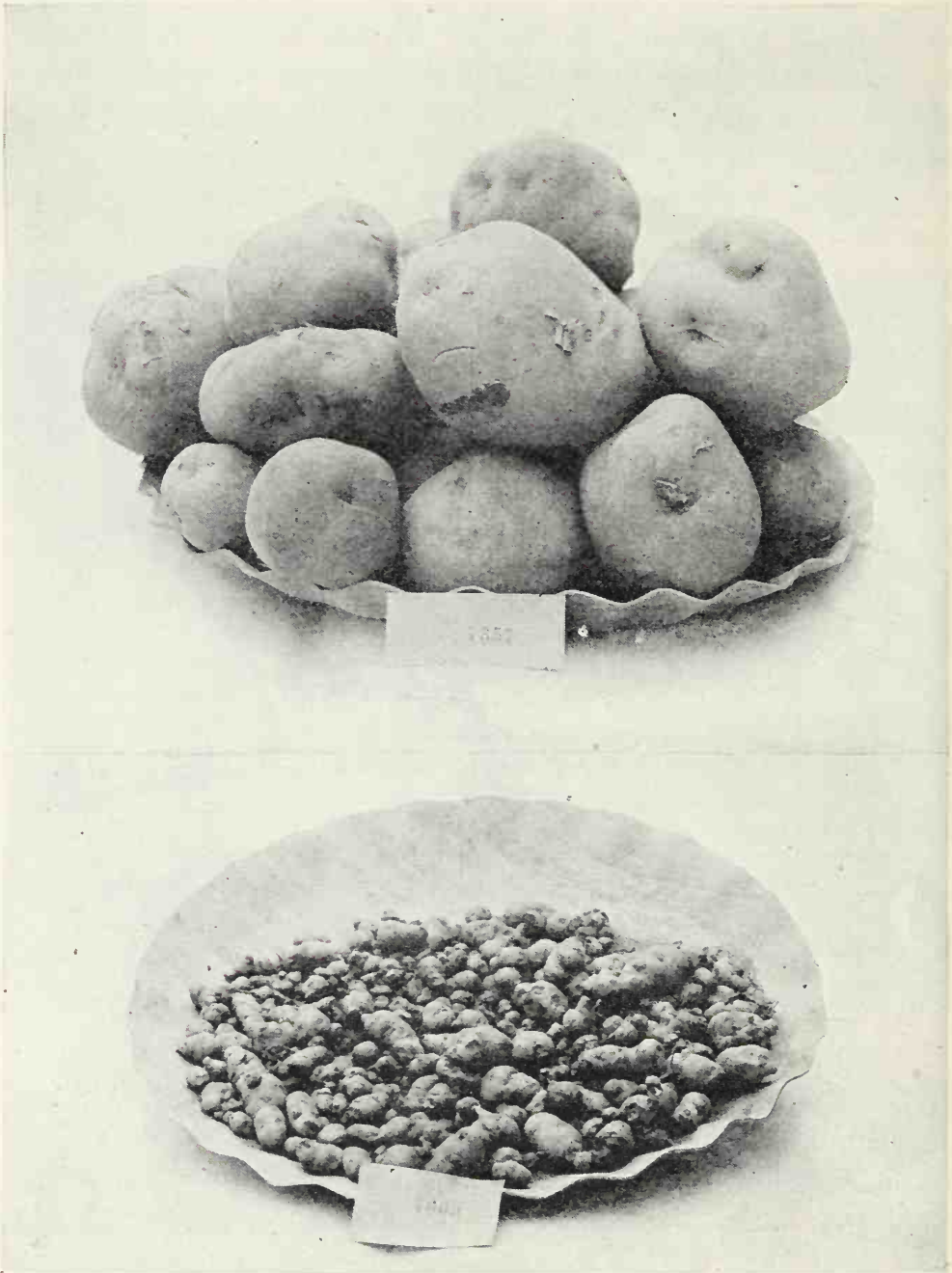


FIG. 211.—The tuber crop from two seedling potatoes. (After Stuart in U. S. Dept. Agr. Professional Bull. 195.)

picture puzzle in the dark. There is no method by which one can predict the results of further crossing without first

genetically analyzing the material worked with. As it is now, on account of the enormous differences between visible characters and breeding behavior, one is often least able to get valuable plants from varieties which show the desired qualities most highly developed. The growing of seedlings from vegetatively propagated fruits and flowers is a fascinating enterprise, which engages the attention of many amateur gardeners. There is reason to expect that better varieties will be the outcome, but the practice of blind crossing does not insure that the results obtained will justify the effort expended.

Results of natural crossing compared with controlled pollinations.—Moreover, there is little evidence to show that those who have made controlled pollinations with definite ends in view have been any more successful than those who have simply sown naturally pollinated seed and picked out the best individuals from the plants grown. C. G. Pringle, of Charlotte, Vt., is one of the few potato breeders who have been able to produce hybridized potato seed from known pollinations. Pringle developed quite a business, selling hybridized seed to seedsmen. It is possible that valuable varieties, of which there is no record, may have come from this seed. Pringle has only one cultivated variety to his credit, Snowflake, which was noted for its high table quality but lacked productiveness. C. E. Goodrich, of Utica, New York, introduced several varieties of potatoes from South America and raised altogether some 8400 seedlings from these, sowing the seed from balls naturally set. In 1861, one of these seedlings, in the hands of Albert Bresee, of Hubbardton, Vt., gave the Early Rose from open-pollinated seed, a variety which is still cultivated but is more worthy of fame for the many fine varieties originating from it.

Twenty-three seedlings, raised from one naturally pollinated seed ball on an Early Rose plant growing at Lancaster, Mass., contained the well-known Burbank potato. Early Rose, in the hands of Alfred Reese, gave birth to the

Early Ohio, again by natural pollination. The Early Ohio is practically the only variety grown at the present time in the Kaw River Valley of Kansas, the Red River Valley of Minnesota, and North Dakota, and is extensively raised throughout the central and middle western states.

The five famous potatoes given to the world by E. S. Carman—Rural Blush, Rural New Yorker, Carman No. 1, Carman No. 3, and Sir Walter Raleigh—have in the past furnished the majority of all the potatoes grown in the northeastern part of the country. These were selected from a lot of seedlings from seed of a number of different varieties grown together in one field and the pollen parent is unknown in every case. The history of the two leading varieties in the East at the present time—Green Mountain and Irish Cobbler—is not positively known, with the implication that they are chance seedlings.

Analyzing vegetatively propagated varieties.—The crossing and selecting of vegetatively propagated plants should go on, but in the meantime there should be an attempt to place the improvement of these plants upon a more scientific basis than it is at present. It is highly desirable that these heterozygous plants should be analyzed in such a way that their good and bad qualities may be more clearly recognized. This can be done by separating out the different hereditary possibilities into fixed stocks of known breeding behavior. Only when this is done can there be any hope of proceeding with any assurance as to the outcome.

Selection in self-fertilized lines, in principle, is the logical method of dealing with such plants. Inbreeding will do for apples and strawberries, carnations, and roses, just what it does for corn. Weaknesses will be eliminated, undesirable qualities weeded out, and valuable characters selected for and held with a certainty that is impossible in any other way. Potentially valuable homozygous strains will be systematically tested, and when valuable hybrid combinations are once obtained vegetative reproduction will assure their permanence and easy multiplication.

The application of selection in self-fertilized lines to many horticultural plants, in practice, is beset with many difficulties, some of which may be insurmountable. Many fruits are so slow in coming into bearing that many years elapse between seed generations, in spite of every effort to speed up reproduction. The length of time necessary to obtain even a small degree of homozygosity is so great as to discourage individuals from making the attempt. This objection would not apply to permanent institutions that are working along this line.

Many of our most valuable horticultural plants are self-sterile and can not be inbred except by sib crosses, thus greatly extending the time required to reach uniformity. Some plants produce seed with such difficulty that even a slight reduction in vigor stops seed formation entirely. In every possible case, self-incompatible plants, whose production is dependent upon proper cross-pollination, should be avoided in selecting material for breeding operations. As was brought out in Chapter XIII, this type of sterility can not be eliminated by inbreeding.

Variation in grafted plants.—Many kinds of fruits and some flowers can not be propagated successfully by cuttings, layers, or other parts of the plant, and therefore have to be grafted or budded on to roots from other varieties. The common practice is to use seedling roots for this purpose. With apples, young trees are grown from seed and dug in the fall, and the roots cut into pieces and joined with the cions taken from the branches of the variety to be propagated. Peaches, cherries, and plums are commonly budded on to seedlings. This practice of grafting or budding introduces a large chance for variation, which has not been given the attention that it deserves. As is well known, the trees of the same variety in an orchard, planted at one time and given equal care, differ in the quantity and quality of the fruit they bear. This variability can be attributed to three different sources:

(1) Environmental influences profoundly affect the pro-

ductiveness of individual trees. Soil heterogeneity is responsible for a large part of this. Differences may exist in fertility, moisture, and physical nature of the soil and subsoil, which are not apparent on the surface. The trees may be injured by insects and disease and in many other ways, or they may have been stunted in the nursery by crowding, mechanical injury, or a poor union of stock and cion. Ordinarily, a tree when given proper care can overcome these handicaps, but it may not always do so, as unfavorable influences are sometimes cumulative. For example, a weakened plant is more easily injured by freezing or sun scald or more susceptible to some insect damage and the ravages of disease than a strong, vigorous plant. But all these factors of the plant's surroundings leave no permanent mark upon the variety, and by the law of chance they tend to equalize themselves. By working with large enough numbers, it should be possible to get equal average production if there were no other variables.

(2) Another opportunity for variation lies in germinal changes or bud mutations in the clonal variety. In the past, much has been written about bud variation. It is now apparent that more attention should be given to the following factor.

(3) Genetic variation in seedling root stocks is an ever-present cause of variation in plants that are grafted or budded. This can have no part in the variability of plants propagated on their own roots or roots of other clones, such as the date palm, grapes, roses, bush fruits, strawberries, and ornamental and flowering shrubs. This would also be true for potatoes, sweet potatoes, dahlias, gladioli, tulips, hyacinths, cannas, irises, etc., but the fact that these plants are reproduced by specialized parts adapted for large food storage brings in another complicating factor, and such plants will be left out of consideration for the present. On the other hand, the citrus fruits, apples, peaches, cherries, plums, etc., are grown on other than their own roots, and since the subterannean part of a plant is as important as

that above ground, the variability due to heterozygosity in the root stocks is a very probable reason for the different results obtained from different trees of the same clonal variety. Dwarf stocks, in comparison with ordinary stocks, for apples and other fruits, are known to profoundly change the growth habit and productivity of the trees grown upon them.

Selection within the clone.—Much of the variability of vegetatively propagated plants has been mistakenly attributed to bud variation, and this has led to the system of pedigree selection of bud wood from plants of good bearing habit. It is significant that bud selection is commonly recommended for the citrus fruits and apples, which are not propagated on their own roots, while it is rarely advocated for grapes or date palms, fruits which are equally long-lived and of great value. This, in all probability, is due to the fact that such plants, being grown on their own roots, are less variable in type and productiveness.

In a seedling apple orchard of 586 trees at the Maine Station, Sax and Gowen have calculated the coefficient of variability in circumference of trunk after ten years' growth to be $32.07 \pm .69$. The trees ranged from 2 to 18 centimeters. Variability such as this is comparable to the diversity in a cross-pollinated seed plant, such as corn. They have also shown that grafted apple trees, as obtained from the nursery, differ greatly in size and that these differences persist in the orchard. If these differences were due solely to environmental influences, such as competition in the nursery, they would tend to disappear in the orchard. Webber has also called attention to the fact that citrus nursery stock shows great variability in size and vigor.

This variation is to be expected, since the stocks upon which these fruits are grafted come from open-pollinated trees which are known to be heterozygous. Most of the apple seedling stocks come from France, where they are grown from seeds of French crab and cider apples. Cions from such seedling stocks have been grafted back on their

own kind of roots and grown by the United States Department of Agriculture at the Arlington Farm, and they show enormous differences in size and vigor.

Clonal selection in deciduous fruits.—Investigations by Whitten in Missouri, Macoun in Canada, Cummings in Vermont, and Crandall in Illinois have shown that differences in individual apple trees are not transmitted. Macoun compared trees grafted with cions taken from heavy-bearing, regular-bearing, and very unproductive trees of the Wealthy variety, and the yields over a period of four years from the three lots of progeny trees gave no significant differences. Cummings, at the Vermont Station, selected cions from productive and unproductive trees of seven varieties of apples. Two hundred and forty-eight trees in all were grown and compared over a period of ten years, with no indication that cions from apple trees of superior performance are any better than other trees of the same variety. Crandall, at the Illinois Station, compared large and small buds from the same trees and buds from different parts of the tree and found no appreciable differences. Similar investigations with strawberries and other fruits have yielded negative results, with the possible exception of the citrus fruits.

Clonal selection in citrus fruits.—Shamel and his coworkers have reported the individual performance records of a large number of orange, lemon, and grapefruit trees. These data show that citrus trees vary in productiveness as do other fruits. They have presented very few critical data to show that high-producing trees transmit high production to their clonal offspring, and unless this quality is handed on, selection of bud stock from high-producing trees is of no value. Trees have been found which have branches of strikingly different appearance, of which one type is productive and the other is not. Buds from these different types of limbs from the same trees have been used for propagation and have given productive and unproductive trees according to the type of the branches from which they came.

Shamel and his co-workers have noted types of fruit, differing in size, shape, character, and thickness of rind, seediness, and differences in regularity of bearing. Some of the differences in type of fruit are apparently transmitted, although no statistical evidence is given in support of this. It is stated that the most desirable strains of grapefruit, lemons, and oranges, when used for propagating, are reproduced in the young trees. The greater uniformity may be due to the fact that the nurserymen are now taking more care in selecting uniform and vigorous root stocks than they did

FIG. 212.—Differences in size of nursery stock of Marsh grapefruit, which have persisted in the orchard, most probably due to differences in the seedling root stocks. (After Webber in Jour. Heredity.)

at first. However, a seedy strain of the same variety of grapefruit that produced fruits fairly free from seeds also transmitted its undesirable qualities.

The most convincing evidence that the common differences found in every grove are due to germinal variations within the clone, would come from undesirable trees which have been top-worked to desirable strains. Although some of these trees were top-worked over eight years ago, no records of their performance have been presented. If the differences are due to diversity in the seedling stocks, there would be nothing gained in top-working them.

Bud mutations in citrus fruits.—Differences in type of citrus fruits are apparently more common than in deciduous fruits. Although a few varieties of apples and plums are considered to have originated as bud sports, the departures from the parental varieties are comparatively small. Such differences as seedlessness, smoothness and color of rind, and regularity in shape of fruit are important in citrus fruits, and if any considerable number of such variations are transmitted through the cion, pedigree selection of superior individual trees may easily be well worth while. It is to be expected that inherent differences in productiveness which are handed on are extremely rare in their occurrence, and until there is more conclusive evidence that such differences are transmitted in the bud wood, extensive records of the performance of individual trees are of doubtful value.

The most convincing evidence as to the occurrence of bud variations in citrus fruits is the production of strikingly different kinds of fruit on separate branches of the same trees. A Washington navel orange tree produced, on separate branches, fruit of at least four distinct types. The Thomson strain of navel oranges is a smooth-skinned variation which originated as a bud mutation. Trees of this type have produced branches which reverted to the original type and also to the rough corrugated type that the Washington navel orange sometimes bears. These variations have been shown to be transmissible.

Tanaka reports the occurrence of a valuable variation in the Satsuma orange in Japan. This has been widely propagated as a new variety and differs from the original stock from which it came in larger size of fruit, smoother rind, earlier maturing, sweeter juice, and greater productiveness. This is a really remarkable instance of a bud variation producing such manifold effects of a progressive nature.

Apparently the same variation has originated independently in six different places. The fact that it is a bud mutation and not a seedling is shown by the occurrence of branches bearing the new form on trees of the original

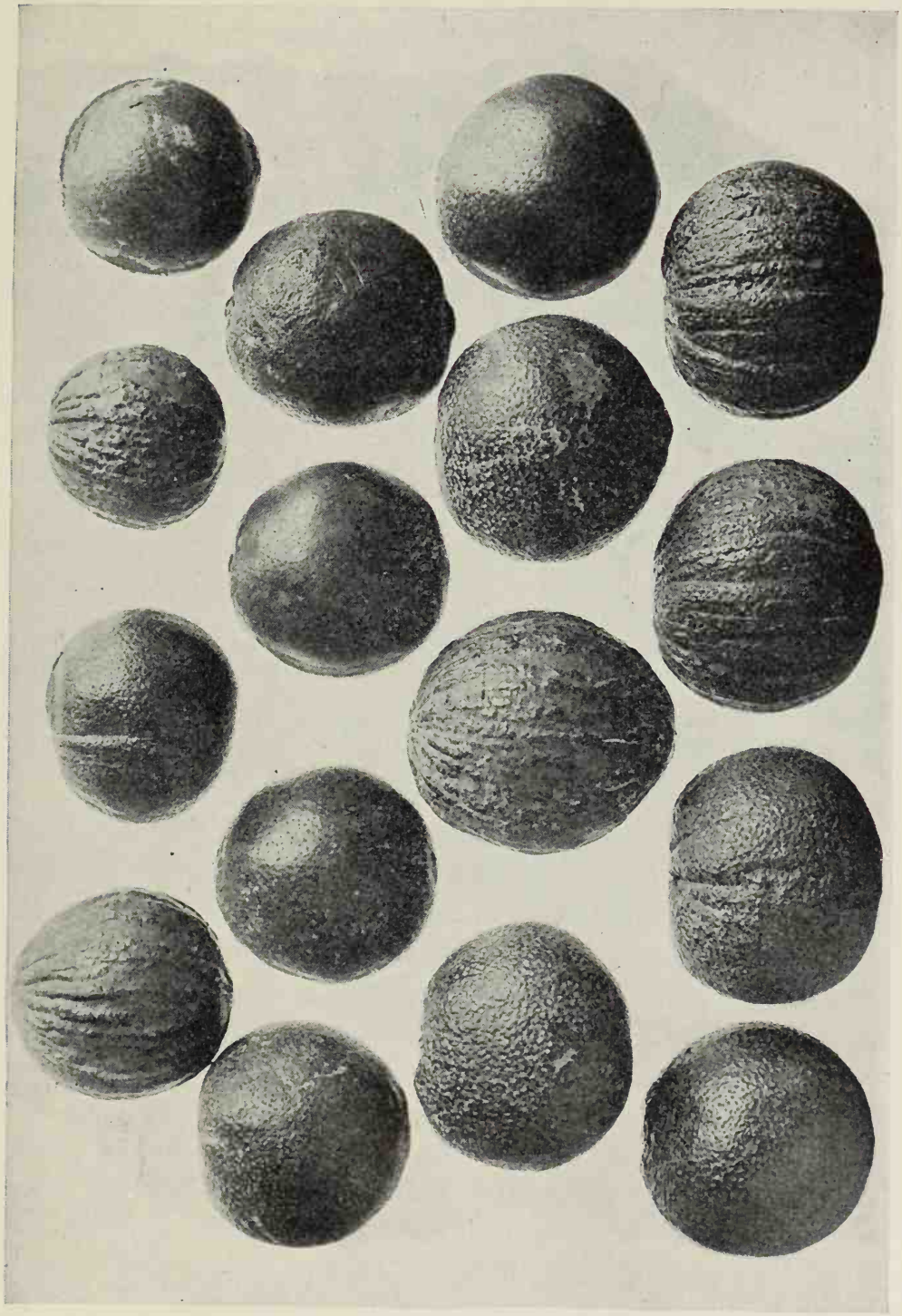


FIG. 213.—Variation in oranges from a single tree. (After Shamel in Jour. Heredity.)

variety. There is also a tendency for the new variety to revert to the old on some of its branches, and trees of the older variety are found in groves which supposedly were all planted to the new variety. That these are due to reversion and not accidental admixtures is indicated by the fact that the off-type trees are always of one variety, the parental one, and not of other varieties. This case is quite similar to the occurrence of nectarines in peaches.

Bud mutations in apples.—Dorsey cites several instances of color variations in apples which have arisen as bud mutations. A dark-colored, almost solid red strain of Duchess, similar to that variety in shape of fruit and habit of growth, was found in a planting of Duchess trees. The same variation also occurred on a single branch of a Duchess tree in another location. Collamer originated as a sport from Twenty Ounce, as did also Hitchings. Both are darker-colored than the original. Banks is a similar variation from Gravenstein. While it is not positively known that these new varieties are bud mutations and not seedlings, the evidence is fairly conclusive that germinal change in somatic tissue is the right explanation.

Nature of bud mutations.—Although the fact of variation in vegetatively propagated plants is conclusive, most of these departures are in minor characters and are usually retrogressive rather than progressive. Because of the ever-present possibility of such variations, propagating wood should be taken from trees that are known to be true to type, healthy, and normally vigorous. Clearly established cases of worthwhile improvement by bud variation are comparatively rare. With the possible exception of those plants which are frequently mutating, it has not yet been established that keeping performance records from individual trees, and propagating from the best of these, offers a sufficient chance for improvement to justify the effort. In any case it must be clearly understood that individual high producers have no value as propagators until their good performance is known to be transmitted to their daughter

plants. Aside from being on the watch for striking, visible changes and carefully testing them whenever they may occur, there is very little that the plant breeder can hope to accomplish with this kind of germinal variation.

Bettering the quality of root stocks.—Instead of spending much time in looking for bud variations, which are entirely fortuitous in their occurrence and are known to be rare, the plant breeder should utilize the far greater opportunity for improvement which lies in bettering the quality and uniformity of the root stocks. The present nursery practice is to bud or graft all the seedlings that make a sufficient growth to be used. The fastest-growing trees are sold as soon as they are large enough. The smaller trees are replanted and grown until they reach saleable size. The orchardist who is buying his trees under present conditions would do well to obtain trees that are known to be one year old from the graft, select the largest and finest of these, and plant in his orchard or reset in nursery rows and grow them to sufficient size. The long life and value of individual trees would justify an additional expense in securing the most vigorous trees to start with. It has not been proved that the most vigorous nursery trees are the most productive or most desirable in other respects, but the indications are that they would be worth more than the weaker trees.

Root stock varieties.—Improvement can undoubtedly be made by developing varieties solely for use as root stocks and selecting them so that they will come truer to type. Since most of these stock plants are as variable as corn and other cross-pollinated seed plants, the difficulties will be just as great. The growing of root stocks from first-generation hybrid seed of homozygous types of proved value would be the best theoretical practice. The expense would be great, as the seed would have to be produced by hand pollination, but this practice would be justified with peaches, plums, cherries, and citrus fruits as long as they can not be satisfactorily propagated on their own roots or

roots of other clones. Although it is somewhat more difficult, apples can be grown on their own roots by employing the nurse root method, as described by Shaw. If trees propagated in this way are as vigorous and long-lived as apples grafted in the usual manner, there is good reason why this should become the prevailing method of propagating this fruit and all other grafted plants which can be

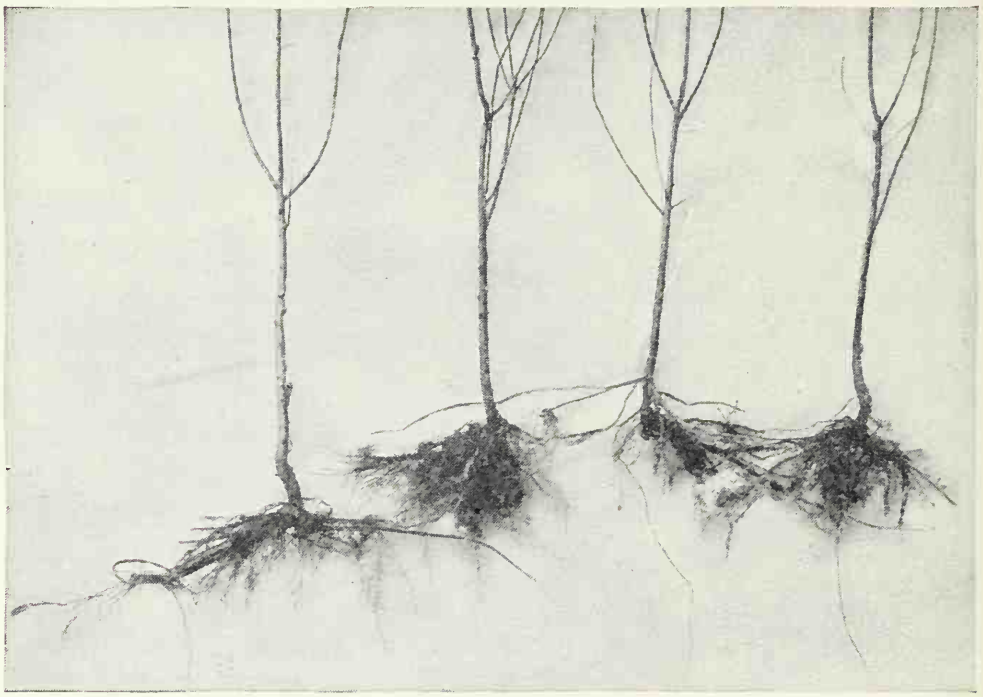


FIG. 214.—Apples propagated on their own roots by the nurse-root method. This eliminates the variability due to seedling stocks. (After Shaw in Massachusetts A. E. S. Bull. 190.)

handled in the same way or similar ways, to eliminate the variable seedling root stock.

Plants not easily propagated by seed.—Potatoes, sugar cane, varieties of oranges and European grapes, and many vegetatively propagated flowers are nearly if not quite seedless. Since Mendelian recombination, made possible by seed reproduction, offers far greater chance for further improvement than germinal variation in vegetative parts, a study of the agencies which promote seed formation in such plants is important. Nutrition, light relation, tem-

perature, all have a prominent part in influencing the production of flowers and the setting of seed. Potato varieties that are commonly seedless form seed balls in abundance in some seasons. Without adequate seed production, all the above plants, together with bananas, pineapples, and others which are entirely seedless, are dependent upon fortuitous bud variations for their further improvement. It is therefore particularly important to know how frequently such variations occur and what proportion of them are in the direction of greater yield and better quality.

Clonal variation in the potato.—East, at the Connecticut Station, examined over seven hundred named commercial varieties of potatoes from this country and Europe, as well as a large number of seedlings, for persistent variations in clonal lines. His observations extended over a period of four years. Every tuber was carefully examined, with the result that eleven variations were found which were transmitted to the daughter tubers. Five of these changes involved a loss of color in the tubers, two were alterations from long to round shape of tubers, and four tubers with deep eyes occurred in shallow-eyed varieties. Many variations which were similar to these, and would have been classed as the same kind of variations, if they had not been tested, did not reappear in the following tuber generations and were either merely environmental modifications or did not affect the buds from which the new plants grew.

None of the variations were progressive; they did not add anything to the value of the plants possessing them. An extensive experiment on selection for higher nitrogen content in the same material did not lead to any change. In view of these results, the outlook for obtaining better strains of potatoes by selection of the more productive plants is not hopeful.

Potential capacity of potatoes to be improved by hill selection.—A study of the variation in yield of plants from the same variety of potatoes has been carried out by Stewart at the Geneva, New York, Station. The variation in yield

of the two halves of the same tuber grown in adjoining hills, compared with the variation in adjoining hills grown from halves of different tubers, gives a measure of the potential capacity of a variety to be improved by hill selection. In the variety worked with, the halves from the same tuber gave a variation in the difference of yield for each pair of 23.4 percent. The halves from different tubers gave a variation of 28.6 percent. The greater variation in the case of the differences in yield between halves from different tubers indicates that this lot of potatoes may be improved by hill selection.

On the other hand, an examination of the mates of the highest-yielding halves fails to show any close agreement. The 31 hills out of 858 which yielded 32 ounces or more had only 5 pairs of which both halves gave this high yield. The remaining 21 pairs gave an average of 33.6 ounces for the high-yielding halves and only 23.5 ounces for their mates in other places in the same field. The single high-yielding halves probably had no hereditary advantage over the others. Although in any hill selection method they would have been chosen as desirable propagators, their higher yield is undoubtedly due to chance location in a situation with more favorable conditions for growth, and these they can not transmit to their progeny. Stewart concludes that " the inherent capacity of a potato plant for tuber formation is so thoroughly masked by the effect of various other factors affecting the growth of the plants as to make detection of the best tubers very difficult. As usually attempted in the hill selection of seed potatoes, it must be largely a matter of chance. While it is undoubtedly true that potatoes often may be improved by hill selection, the improvement can not be carried to a high degree of perfection until better methods than we now possess have been devised for ferreting out plants having capacity for high production."[1]

East quotes Sutton as saying, " I have no hesitation in affirming that there is no potato in commerce in England,

[1] Geneva, New York, Agr. Exp. Sta. Bull. 489, p. 50.

and I might say in Europe, which owes its origin as a distinct potato to bud variation in any form whatever."

Importance of hill selection to prevent degeneration.—Even if no systematic improvement can be looked for in this way with the potato, hill selection is worth while to prevent degeneration due to various causes which seriously cut down the yields of potatoes. There are two factors which have a profound effect upon the yielding power of potatoes. One of these is the effect of the climate and the other the accumulation of disease. The potato, which carries an extraordinarily large amount of stored food in the specialized part used for reproduction, is markedly affected by pathological troubles. Other plants, such as the bulbous flowers, are similarly affected.

The potato is adapted to a cool, moist climate. Although it can be grown in nearly all parts of the country, including the irrigated districts of the hot, dry, desert regions of the Southwest if it is planted at the proper season, the potato is usually unable to retain its yielding ability, outside of the most favored districts, for more than one or a few seasons. It has therefore become a common practice to plant northern-grown seed. The reason for this degeneration is not clearly understood. It is apparently not germinal in the way that unfavorable mutations sometimes occur in this and other organisms. There is some evidence, obtained by Macoun at the Central Experiment Station in Canada, to show that plants which have been reduced in yield can be restored to their former vigor when returned to a suitable climate and kept there long enough to regain the full size of tuber and normal growth. The evidence is conflicting on this point. The falling off in yield in southern regions has some connection with the maturity of the tubers. Second-crop tubers grown late in the season, which do not reach full size, can be successfully grown in some localities for seed purposes.

The second factor in degeneration, that of accumulated disease, is the most baffling and has not yet been satisfactorily explained. Various fungous and bacterial diseases

of potatoes, such as Black Leg, Scab, Fusarium Wilt, Rhizoctonia, Powdery Scab, and Wart, annually cause considerable reduction in yield and quality and the organisms which cause the trouble are carried in the tubers. In addition to these diseases which have been thoroughly investigated, a number of abnormal types are frequently found in potato fields, particularly in an unfavorable season or under poor cultural conditions. These pathological variations, such as leaf roll, mosaic, wilt, curly dwarf, and spindling sprout, are transmitted from generation to generation. There is no evidence to show that affected plants can be brought back to normal health. Recent investigations show that these troubles are also due to parasitic organisms, but these have not been positively identified. It seems that these diseases are probably different manifestations of similar troubles. Whatever may be the cause of these degenerative diseases of potatoes, it is a matter of prime importance to prevent their appearance and spread as far as possible.

Value of hill selection.—For seed purposes, Stewart recommends growing potatoes in fields removed from other potatoes, and planting with seed selected in the field from good-appearing hills. All weak plants and particularly those showing mosaic, leaf roll or wilt should be removed during the growing season. When these precautions are taken, all tubers over one ounce in weight may be used for planting. Other things being equal, small tubers are more productive than large ones, another indication of the influence of immaturity upon yield. Unless these precautions are taken, as Stewart points out, the planting of small tubers will tend to increase the number of weak and degenerate plants and the final result will be disaster.

Summary.—To sum up the methods for plant improvement the first consideration is whether the plants are naturally self-pollinated or naturally cross-pollinated. This gives a clue to the germinal condition of the plants with respect to homozygosity or heterozygosity. The individual members of a self-fertilized variety, although usually

homozygous and therefore stable within themselves, are seldom all exactly alike. Such diverse forms can be separated into a number of sub-varieties which are uniform. To do this, the simplest and most effective procedure is to propagate from individual plants and test their progeny. The greatest uniformity is brought about in this way and the opportunity is offered to obtain an improvement in valuable qualities, particularly in those which are not positively correlated with reproductive ability. Recombination of characters from different races and different species by crossing, followed by selection until uniformity and constancy are obtained, is the means of originating radically new varieties.

Cross-fertilized plants must be handled in such a way as to maintain full vigor and at the same time permit a thorough control of the heredity from the pollen parent as well as the seed parent. Selection in self-fertilized lines, continued until homozygosity is reached, and followed by some system of crossing, offers the best means of doing this. In this way undesirable qualities, which are hidden by cross-fertilization, are most easily eliminated, and the highest expression of the particular characters desired is obtained. Vegetatively propagated plants, because of their heterozygous condition, are handled in the same way as cross-fertilized plants and have the added advantage of maintaining any valuable hybrid combination of characters by means of their special mode or propagation.

First-generation hybrids, between varieties of either self-fertilized or cross-fertilized plants, offer a practicable means of increasing yields in special instances where the cost of producing the seed is not prohibitive.

Vegetative mutations offer the only means of improving those plants which are unable to make seed, and are a possible source of valuable variations in all kinds of plants; but, on account of their rare occurrence, selection within the clone is only worth while with those plants which show frequent mutations.

CHAPTER XV

METHODS FOR ANIMAL IMPROVEMENT

HISTORY does not go back far enough to record the beginnings of animal husbandry. Some of the earliest carvings depict man with his beasts of burden. The great differences which exist between domesticated animals and their nearest wild relatives are evidences of the long time during which the former have been under the guiding hand of man. Agriculture was firmly established before any of the important mechanical inventions were made available, and while there has been continued progress in the latter field, animal breeding proceeds in much the same way as it did four thousand years ago. The belief in maternal impressions, mentioned in Genesis, is still often held, along with many other opinions that have no foundation in fact. The betterments that have been made in animals for man's uses are the result of the application of the simple formula: selection of the best for breeding stock.

The beginning of pedigree registry.—From the first, selection has been based largely on individual appearance and performance. There is at least one instance, however, in very early times, when attention was paid to the ancestry of the animals used for breeding purposes. The Arabs, over thirty centuries ago, developed a breed of horses whose qualities of speed and endurance are still highly valued. They took pride in tracing the pedigrees of their horses back to famous founders of the race, and valued their favorite horses not only for their own merits but for the qualities of their progenitors.

There is no other record of the systematic application of

a pedigree registration system until the middle of the eighteenth century in England. At that time, the red, black, and pied short-horned cattle of northeastern England, interbred with bulls from Holland, had achieved more than local fame. Individuals of outstanding merit were known by name, and breeding stock was valued for the ancestry back of it as well as for its own individual characters. This led in time to the system of recording pedigrees, which was finally incorporated into the publication of the English herd book. The first volume of this was published in 1822. Herd books for other breeds of cattle and for other classes of livestock appeared soon afterward.

Value of breeding stock lies in progeny performance.—The development of the written record of descent followed the realization that the value of an animal for breeding purposes consisted in its ability to transmit good qualities rather than in its own appearance. It was noted that individuals of the same size and conformation and of equal value for market purposes differed greatly in their ability to beget offspring that were uniformly good. An examination of their pedigrees showed that back of the good performers there was a record of stock above the average, whereas the poor performers had somewhere in their ancestry individuals of inferior quality.

Empirical nature of breeding practice.—The pedigree registration system has had great value in making the important breeds of farm animals as we see them to-day. Up to the present time, the new knowledge of genetics has contributed little to this advance. The best practice in mating animals was learned by many patient trials, of which the outcome was not always satisfactory. This has led to a large fund of empirical knowledge, which is often very confusing to the beginner unless he is acquainted with the principles that govern the transmission of inherited characters and knows the important distinction between the two different kinds of variations: those which are transmitted and those which are not.

Animal breeding an art.—The possession of this knowledge does not assure success in practice. Animal breeding is an art in which one can become proficient only after acquiring experience and familiarity with the material handled. Skill in judging animals is necessary. Without the ability to estimate accurately the valuable qualities and defects of the individual to be chosen for breeding purposes, one is helpless. Knowledge of feeding and proper equipment for caring for animals are essential. Unless they are grown in such a way as to bring out their full capacities, selection can not be made intelligently. A milk cow may have the potential ability to produce a thousand pounds of butter fat a year; but if she is weakened by disease, injured by exposure, or fed an insufficient or improper ration, there is no likelihood that she will do any better than a cow of much inferior breeding. Although qualities which are brought out by good care and good food are not transmitted unless they also have a basis in the germplasm, animal breeders must proceed as if acquired characters were inherited. In all the meat animals, it is absolutely necessary to bring out the best growth in order to have an idea of what the hereditary possibilities are, since it is largely these fine matters of size development that give an animal meat value.

Knowledge of the reproductive process in the different races of farm animals is essential to the success of any animal breeding enterprise. An acquaintance with the past history of the breeds is useful in guiding their future development.

Where the science of genetics can help.—Animal breeding as it is now practiced is still far from reaching the plane of efficiency which is possible by the application of the principles already established. This failure in efficiency is due to a misconception as to the way in which selection operates. It is generally held that selection has a creative power and, if carried on rigidly and persistently, will result in continued progress in any desired direction. As has been brought out in previous chapters, this is not the case.

Individuals differ in their ability to perform. Some will transmit this ability to a part or all of their offspring and some will not. A uniformly good record on the part of all the recent ancestors increases the chances that this ability will be continued into later generations. Herein lies the value of the pedigree registration system. However, on account of the great germinal variability in all crossbred animals, even a satisfactory ancestral record does not insure the ability to transmit these qualities. Mendelian recombination is always taking place, and the possibility of losing the particular combination of factors which makes high production is always present.

The progeny performance test.—It is now clear that continued success in animal breeding is closely dependent upon the application of the progeny performance test. This is well brought out by experiments on egg production carried out by Pearl and others at the Maine Station. During the first part of the selection experiment, hens which had laid 160 or more eggs in their pullet year, as shown by the trap nest records, were chosen for mating with males whose dams had laid 200 eggs or better. This rigid selection was continued for nine years with representative Barred Plymouth Rocks obtained from leading poultrymen. During the long period of selection, no increase in the average egg production of the flock was obtained. The hens maintained full size and vigor, and the numbers employed were large enough so that the loss of vigor which might have been due to close mating, was not responsible for the failure to raise the egg yield. The selected birds were mated at random. The system followed was essentially mass selection, but was carried out more carefully than the general poultryman conducts his breeding operations, because the complete egg record of every hen was known. From the results it is evident that selection based solely upon individual laying capacity has in most cases already reached about the limit that is possible by this system of selection.

After mass selection had been practiced in this way, without results, for nine years, there was a radical change in method. The hens were chosen not only for their ability to lay a large number of eggs, but also for their ability to produce daughters whose egg-laying capacity was high. Similarly, the males were chosen after the egg records of

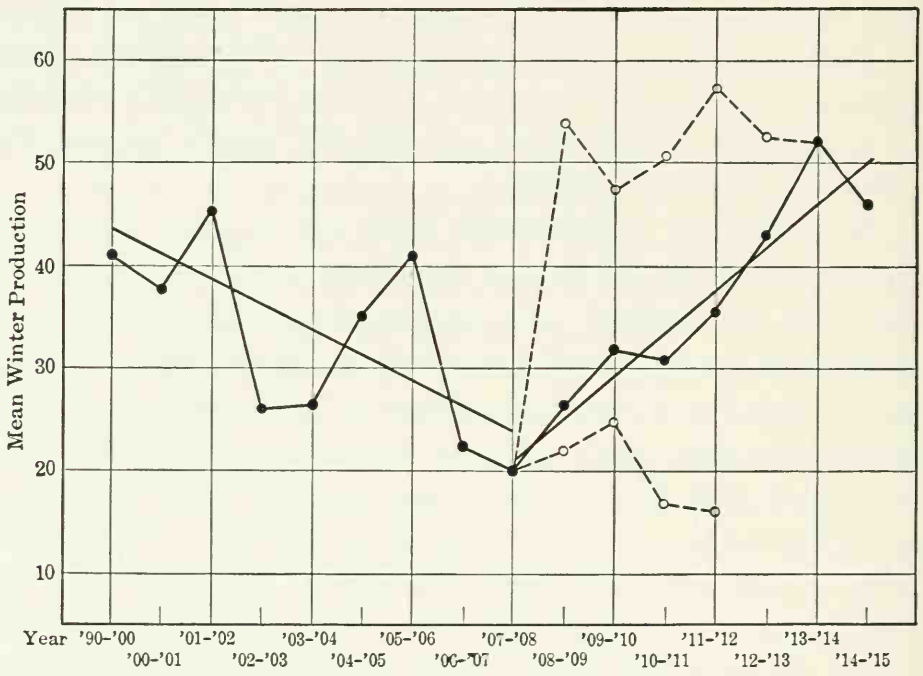


FIG. 215.—A graphic representation of the results of selecting for high winter egg production. During the first nine years, mass selection, during the last eight years, genotypic selection, based on progeny performance. The broken lines show the results from two strains selected for high and for low winter egg production. (After Pearl in American Naturalist.)

their daughters were known. Selection was thus based primarily on their ability to transmit uniformly high production to all their offspring. During the eight years this system was applied, there was a rapid increase in the number of eggs laid during the winter months, which was the principal object sought for. Selection was also carried on in the opposite direction, and a strain of poor layers, differing markedly from the high producers, was

quickly established, although all were fed and housed alike.

Why mass selection is not fully effective.—Pearl has obtained evidence that the high winter egg production in Barred Plymouth Rocks, as contrasted with the poor laying capacity of Cornish Indian Game fowls, is due to definite hereditary factors for fecundity, which are transmitted and recombined in the same way as other Mendelian factors. The ability to lay is, of course, greatly affected by environmental influences, such as housing and feeding, and is undoubtedly modified by other hereditary factors which affect nearly all the characters of the hen. It is therefore easy to understand why mass selection is not more effective. A good egg record may be made simply as a chance deviation from the general average of the flock, due possibly to the fact that the hen was exceptionally strong and healthy and remained so from the start without having all the hereditary factors for high egg production. Such a hen will not transmit her ability to any of her offspring when mated with a male of similar constitution. Another hen may be heterozygous for the factors determining high egg yield, and therefore will transmit her ability to lay to only a part of her offspring. The best results can be obtained only by having both males and females homozygous for all hereditary factors for high egg production. This necessitates the recording of individual matings and the testing of the performance of the offspring. Those matings which give uniformly high producers show which individuals are the most valuable for breeding purposes.

Appearances not associated with utility.—Mass selection is undoubtedly of value in poultry breeding in maintaining egg production at the comparatively high level it has already reached, but any further appreciable increase in average laying capacity by continued selection in this way is not to be expected. Selection is more effective when based directly upon egg production than when based upon other characters, which may or may not be correlated with laying

ability. Certain characters which have been used in judging livestock are actually antagonistic to high production. As brought out in Chapter VIII, Blakeslee and Harris have found that there is a high degree of association between the color in the ear lobes, beaks, legs, and skin of hens and their egg record during the preceding months. A lack of

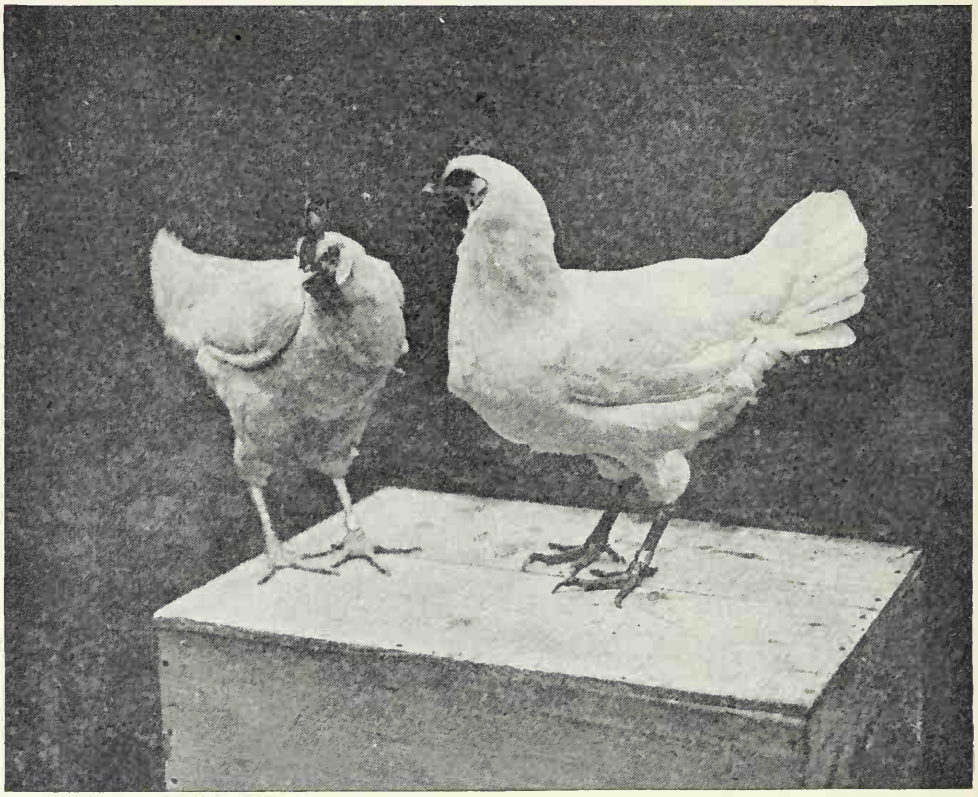


FIG. 216.—The hen on the left laid more eggs but scored lower on show points than the better appearing hen on the right. Note the heavily pigmented shanks of the poor layer. (Courtesy of the Connecticut Agricultural College.)

yellow pigment is characteristic of those hens which have been laying regularly, while non-layers show much more color. Apparently the pigment, when not used in the eggs, accumulates and is stored in various parts of the body. The standards for White Leghorns, as one instance, require white ear lobes and yellow beaks and legs in both sexes. Such a combination is inconsistent and difficult of attainment if not largely impossible. Yellow color in beaks and

legs during the seasons of active laying indicates poor layers.

Too close attention to fancy points in many breeds of all kinds of farm animals has worked to the detriment of pure-bred livestock. The aim of animal breeding, which is to increase production, should always be kept uppermost. Many breed characteristics, which have no direct importance for production, do serve to a certain extent as indicators of breeding and for that reason have value. All the standard breeds of poultry have certain definite combinations of plumage, color, pattern, and comb shape, which permit their ready classification and show at once whether or not their ancestors have conformed to certain standards. The same is true of practically all breeds of farm animals.

Value of dairy bulls measured by milk yield of their daughters.—The value of selection based upon performance has been proved for poultry and is equally applicable to the larger animals. Performance may be measured by the scales, in weight of wool or dressed meat, in the milk pail, on the race track, or in the show ring. With dairy cattle, the value of a bull is shown in his ability to increase the milk or butter-fat production of his daughters over that of their dams. In making such a comparison, the conditions of feeding, care, and housing must be as nearly equal as possible, and allowances must be made for differences in age of the cows at the time the milk records are taken.

Pearl, Gowen, and Miner have examined the progeny performance record of 224 Jersey Registry of Merit sires with this point in view, and found that 105 of these bulls, less than one-half, have raised the milk production of their daughters over the daughters' dams. Out of 111 Holstein–Friesian sires having two or more year-test daughters in the Advanced Registry from tested dams, 65 increased the milk yield of the daughters. To be strictly fair, such a comparison should be made with bulls which have been bred to the same cows or cows of equal capacity. There is probably a tendency to use the most valuable sires with the

highest-milking cows, and it is obviously more difficult to raise milk yield in such a case than where the mating is made with a low producer. In the investigations cited, allowances were made for this by classifying the cows into four grades according to their production, and the ability of the sire is shown by the production of his daughters from each class of cows.

Untested bulls largely used.—In Maine, Pearl has gathered statistics which show that 85 percent of the dairy sires used are under four years and ten months of age. This state of affairs is probably typical of the entire country. The distribution in respect to age is given in Table XLIV.

TABLE XLIV

THE AGE OF BULLS USED IN MAINE AS BREEDERS

Data from Pearl, in Maine A. E. S. Bull. 258

Age in Years	Number of Bulls	Percent
1	213	22.03
2	252	26.06
3	209	21.61
4	149	15.41
5	52	5.78
6	53	5.48
7	24	2.48
8	8	.83
9	3	.31
10	..	..
11	..	..
12	4	.41
Total	967	100.00

Since it takes at least four years before the milk-producing capacity of the daughters of a bull can be tested, more than three-fourths of the calves in the country are sired by bulls whose ability to transmit milking qualities is wholly unknown.

Age of sires of leading Jersey cows.—In contrast to these figures stands the age at time of service of the sires of some of the leading Jersey cows. Out of 32 cows, only one was sired by a bull under one and a half years. Sixty-five percent were sired by bulls over three years. This does not mean that old sires are necessarily better than young ones. The production records of Jacoba Irene, sired by a bull of one year, and of Eminent's Bess, whose sire was only two years old, indicate that age is not essential to the transmission of milking capacity. Both of these were world's champion Jersey cows at one time. F. R. Marshall is authority for the statement that the average age of the sires of 2.10 trotters was practically the same as that of all standard bred horses of the same period. F. S. Putney analyzed the records of the Jersey herd of the Missouri Station and found no relation between age of dam and butter-fat record. The results do show clearly that those Jersey breeders who are producing world's record cows are using tested sires whose abilities to transmit valuable dairy qualities to their offspring is known by actual previous experience.

Dams hereditarily as important as sires.—The advantages of known breeding capacity apply as well to the dams as to the sires. Since transmission is the same through one sex as the other, it is important that the dam should also be selected on the basis of the performance of her offspring. However, this is more difficult, as the number of young from one individual is not sufficiently large to afford a reliable comparison until the dam is too old to be of much further value. Because the males are used with a large number of females, it is justifiable that the most attention should be paid to them. But a sire, no matter how valuable he may be, can not make up for a lack of good breeding in the dams with which he is mated.

Comparative results from Holstein sires.—The offspring of particular individuals may differ greatly. The sire with the capacity to produce uniformly good offspring is the one

that is the most valuable. This is equally true whether the animals are being produced for breeding purposes or for the market. Phenomenal individuals are occasionally obtained from individuals whose other offspring are much less valuable or even decidedly inferior. This is well brought out in a tabulation of Holstein sires that have one or more daughters whose record is equivalent to 1000 pounds of butter fat, as given in Table XLV from figures compiled by Hunt.

TABLE XLV

LIST OF HOLSTEIN-FRIESIAN SIRES HAVING ONE OR MORE EQUIVALENT TO 1000 POUND BUTTERFAT DAUGHTERS

Data from Hunt in Journal of Heredity

Rank	Name of Sire	Number A. R. O. Daughters	Number Proven Sons	Number Daughters Dams of Tested Daughters	Number Equivalent to 1000 Pound Daughters	Number Equivalent to 800 Pound Daughters	Number Equivalent to 600 Pound Daughters	Year of Birth
1	King Segis Pontiac Count	29	8	4	5	12	13	1911
2	King Hengerveld Aaggie Fayne	34	4	16	3	4	5	1908
3	Sir Pietertje Ormsby Mercedes	68	23	14	2	16	42	1907
4	King of the Pontiacs	251	160	80	2	14	25	1905
5	Pontiac Aaggie Korndyke	58	21	21	2	9	13	1905
6	King Pontiac Champion	94	25	25	2	8	22	1908
7	Friend Hengerveld DeKol B. Boy	46	5	20	2	4	4	1901
8	Aaggie 3d's Wayne Paul DeKol	19	1	25	2	3	4	1900
9	Sir Veeman Hengerveld	103	13	53	1	6	8	1904
10	King Walker	67	25	25	1	5	10	1905
11	Colantha Johanna ad	126	92	33	1	4	9	1903
12	King Mead of Riverside	24	1	6	1	3	13	1908
13	Prince Gelsche Walker	30	6	2	1	3	7	1910
14	Maplecrest Pontiac Hartog	26	4	4	1	3	4	1908
15	King Segis Beets	47	18	20	1	3	4	1906
16	Johanna Rue 3d's Lad	49	30	40	1	3	3	1899
17	Alcartra Polkadot Corrector	22	17	21	1	3	9	1902
18	Sir Korndyke Hengerveld DeKol	45	36	21	1	2	5	1905
19	Pontiac Korndyke	147	119	96	1	2	5	1898
20	Sir Johanna Canary DeKol	16	2	13	1	2	3	1906
21	King Beauty Pietertje DeKol	9	1	3	1	2	2	1907
22	Cornucopia Waukasha Prince	11	3	13	1	2	2	1904
23	McKinley Hengerveld DeKol	16	3	13	1	1	3	1907
24	Dutchland Sir Pietertje Hengerveld	23	13	5	1	1	3	1907
25	Pontiac Appollo	50	14	18	1	1	2	1905
26	Iowanna Sir Ollie	2	0	0	1	1	2	1913
27	Sir Ormsby Skylark	11	1	8	1	1	2	1907
28	Ona Pontiac DeKol	1	0	0	1	1	1	1908
29	Flora Brank Paul Pledge	8	0	9	1	1	1	1903
30	Paul DeKol of Royalton	8	2	5	1	1	1	1903
31	Sir Hengervel l DeKol Abbekerk	11	0	0	1	1	1	1908
32	Linden Butter Boy Pietertje	9	0	6	1	1	1	1907
33	Butter Boy Segis Korndyke	17	0	5	1	1	1	1908
34	Sir Jolie Johanna 4th	5	0	2	1	1	1	1903
35	Sir Ormsby Burke Segis	21	1	10	1	1	1	1908
36	Admiral Urmagal Burke	4	0	0	1	1	1	1913
37	SeKol Beets Segis 4th	9	1	1	1	1	1	1910
38	Soldene Beets Butter Boy	1	0	0	1	1	1	1910
39	Sir Hengerveld Clyde	1	0	0	1	1	1	1912
40	Leda Hengerveld Sir Plebe	3	0	2	1	1	1	1904

There are two bulls listed, both born in the same year and having approximately the same number of tested daughters. King Mead of Riverside, with 24 tested daughters, has 1 with a record equivalent to 1000 pounds of butter fat and 13 equivalent to 600 pounds. Sir Ormsby Burke Segis, with 21 tested daughters, also has 1 equivalent to 1000 pounds but only 1 equivalent to 600 pounds. In the former case, a large number of daughters are in the high-producing class, whereas in the second there are only a few of these, while each have approximately the same number of tested offspring.

Where young and untested sires of the larger animals are used, the herd may be entirely changed for the better or for the worse before the value of the sire is known. This justifies the practice of mating all young males with older females of known breeding capacity, and holding them in reserve until the character of their offspring is known. This is often difficult to do and is always costly, but in view of the serious consequences of using an inferior sire this procedure is fundamentally sound.

Estimating appearance and pedigree.—Before the breeding ability of an animal is known, the only way of estimating its value is by its appearance and pedigree. Both should be given due weight. The animal itself must conform as closely as possible to the best standards of the breed. As has been repeatedly emphasized, however, this alone will tell very little about its value for breeding. The ability to transmit good qualities to a large part of the following generations depends on the degree of homozygosity with respect to dominant qualities which make for high ability. This in turn depends upon the extent to which the ancestors making up the pedigree are alike. Varied ancestry, even though each representative is good in itself, means that the offspring will be variable and unable to transmit their own characters to more than a few of their progeny in turn. An illustration of breeding to bring about fixity of type is given in the pedigree of Comet, shown

in Table XLVI. This famous bull of Charles Colling traces in every line to the bull Foljambe. Comet was one of the most famous of the early Shorthorns.

TABLE XLVI

THE PEDIGREE OF CHARLES COLLING'S FAMOUS SHORTHORN BULL COMET. NOTE THAT EVERY ANCESTOR IN THE PEDIGREE OF EITHER OF THE PARENTS APPEARS ALSO IN THE PEDIGREE OF THE OTHER

A_1	A_2	A_3	A_4
Comet	Favorite	Bolingbroke	Foljambe
			———
		Young Strawberry	Dalton Duke
			Lady Maynard
	Phoenix	Foljambe	———
			———
		Lady Maynard	———
			———
	Young Phoenix	Favorite	Bolingbroke
			Foljambe
			Young Strawberry
		Phoenix	Foljambe
			Lady Maynard
	Phoenix	Foljambe	———
			———
		Lady Maynard	———
			———

Fractional pedigrees.—The conception of heredity as a blending process, whereby the influence of each individual upon later generations is evenly reduced in force as the number of generations, by which it is removed, grows greater, is often seriously misleading. This is the idea conveyed in fractional pedigrees. For example, in common usage a " full-blooded " Shorthorn mated to a Hereford of equal purity gives a " half-blood," which, crossed back to either breed gives " three-quarters " Shorthorn or Hereford as the case may be, and so on.

As a matter of fact, inherited characters in animals are so numerous and complex, and deal with so many and such intricate traits and individualities, that, as a rough rule, the fractional expression fits the observed facts fairly well, particularly in wide crosses where a large number of hereditary differences are involved. Moreover, it describes accurately the state of affairs when large numbers are averaged together, but in particular cases this method of designation

fails entirely to give the true state of affairs. For example, suppose we take the cross of Aberdeen–Angus PPBBww, to Herefords ppbbWW. In this case, let " P " represent the polled character and small " p " the horned, capital " B " the black coat and " b " the red coat, " W " the white markings and " w " the solid color. Then P, B, and w are Angus genes and p, b, and W are Hereford genes. Taking F_2 and computing the percentage of Angus and Hereford factors in each individual we get the following:[1]

	Percent Angus	Percent Hereford
1 PPBBWW	67	33
2 PPBBWw	83	17
2 PPBbWW	50	50
2 PpBBWW	50	50
4 PPBbWw	67	33
4 PpBBWw	67	33
4 PpBbWW	33	67
8 PpBbWw	50	50
1 PPBBww	100	0
2 PPBbww	83	17
2 PpBBww	83	17
4 PpBbww	67	33
1 PPbbWW	33	67
2 PPbbWw	50	50
2 PpbbWW	17	83
4 PpbbWw	33	67
1 ppBBWW	33	67
2 ppBBWw	50	50
2 ppBbWW	17	83
4 ppBbWw	33	67
1 PPbbww	67	33
2 Ppbbww	50	50
1 ppBBww	67	33
2 ppBbww	50	50
1 ppbbWW	0	100
2 ppbbWw	17	83
1 ppbbww	33	67

While this generation averages 50 percent Hereford and 50 percent Angus characters, we have as a matter of fact, with the three characters under observation:

[1] For this illustration of the actual working of separate factors I am indebted to E. N. Wentworth.

Number of Individuals	Percent Angus	Percent Hereford
1	100	0
6	83	17
15	67	33
20	50	50
15	33	67
6	17	83
1	0	100

This is easily understood from the alternate way in which Mendelian inheritance works through the chromosomes, as contrasted with the erroneous view of inheritance through the blood. The fact that this diversity actually occurs renders a fractional designation of the whole lot of second-generation hybrid animals as " half-blood Aberdeen Angus, Hereford " obviously inaccurate. This error is not serious, however, as all stockmen appreciate the fact that great variation results from wide crossing and that individuals in the same progeny may differ as much as the original types that were put into the cross. A point which is not fully appreciated in this connection is important in regard to the value of pedigrees of pure-bred stock, and particularly of those which contain famous individuals somewhere in the rather remote family tree. Since any ancestor beyond the immediate parents can be absolutely eliminated from the hereditary make-up of any particular individual, something more than the pedigree must justify a valuation based upon the qualities of an ancestor, which may or may not have been handed on.

Elimination of ancestors.—Since heredity is carried in the chromosomes, as far as known at the present time, the complete elimination or entire recovery of any particular ancestor depends upon the chance assortment of these chromosomes. If we take the simplest possible illustration, a hypothetical animal with only one chromosome pair, and assume that there is no crossing-over, then the constitution of any one individual, in respect to transmissible characters possessed by its grandparents, would be according

to the chance allotment of the four different chromosomes, as shown in Fig. 217. One of the two members of the chromosome pair possessed by individual *I* came from each of the two parents; that from the sire, *S*, would be originally from either grandparent 1 or 2, but never from both. In the same way, the chromosome handed on through the dam, *D*, might come from either 3 or 4 but never from both. The composition of individual *I*, with respect to chromosomes possessed by the grandparents, could be 1–3, 1–4, 2–3, or 2–4. Hence, in all the offspring produced by the mating of *S* and *D*, any one grandparent would be represented in only one-half of the lot. For example, ancestor 2 would furnish part of the inheritance for half of the offspring, but in the other half 2 would be entirely

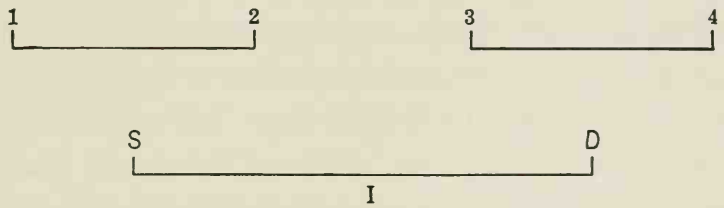


FIG. 217.—The pedigree of an individual, I, showing his relation to the two parents and four grandparents.

eliminated. Therefore, any qualities peculiar to 2 or its ancestors, for any number of generations back, will never reappear in that half of the progeny which lack the 2 chromosome. As far as the inheritance possessed and handed on by those individuals is concerned, that ancestor might never have existed.

With a fairly large number of chromosomes, as in all domestic animals, together with more or less interchange between the two members of a chromosome pair, the matter is far more complex. The possibility of any recent ancestor being wholly regained or entirely lost is very much less; but some of the offspring will have more of the heredity of particular ancestors than will others, and there will be others which are correspondingly lacking in that heredity. Of this there can be no question.

Calculating ancestral elimination.—Laughlin gives a way of calculating the probable influence of any particular ancestor upon a given individual with varying numbers of chromosomes. Of necessity, crossing-over and other complications due to differences in the sex chromosomes are left out of consideration. The ratio of those individuals in which a particular ancestor is entirely eliminated is found from the formula

$$1 : \left(\frac{2^{p-1}}{2^{p-1}-1}\right)^{n}$$

where p is the ancestral generation and n is the number of chromosome pairs. For example, with an animal such as the pig having ten chromosome pairs, any one of the four grandparents, as far as inheritance from them is concerned, will be dropped out from 1 out of every 1024 individuals of the generation under consideration. Going back only a few generations further, the chances for complete elimination become much greater. The great-great grandsire or dam will be entirely unrepresented in a little more than 26 percent of the progeny, when no close mating is practiced. While there is a lessening of the influence from some of the ancestors, there is a corresponding concentration of the heredity from others. Crossing-over tends to reduce the chance for total dropping out or regaining the inheritance from particular individuals. When inbreeding in any degree is practiced, the number of different ancestors is reduced and the chances that the qualities from particular progenitors will be lost are less, and the expectation is in direct proportion to the degree of consanguinity.

The fact that in every herd of cattle, flock of sheep, and drove of hogs, a certain number of individuals lack completely any inheritance from particular ancestors in any given ancestral generation, so that for them those ancestors might never have existed except that they were a part of the living machinery which produced the present generation, is a matter of great importance in studying pedigrees. It

is essential that real worth accompany good breeding as a pre-requisite for registry. No one can injure a breed more than by permitting genotypically inferior animals to enter, even though they come from eligible matings. Undue consideration given to remote ancestors, whose good qualities may or may not have been handed on, is not justified in the light of present-day knowledge of the process of inheritance.

Antagonism between largest growth and control over the heredity.—Because of the element of chance in the transmission of inherited qualities, there will always be more or less uncertainty as to the breeding value of any individual. Only by bringing sexually reproducing organisms to a fairly high degree of homozygosity can there be any possibility of successfully predicting the outcome in particular matings. But, under the conditions actually existing in livestock, homozygosity generally means loss of vigor. There is, therefore, antagonism between the largest growth and any high degree of control over the heredity, and in the present practices of animal breeding there is no way of completely overcoming this handicap.

Undesirable characters persist in even the most carefully selected purebred animals, as is well known. The red color in Holstein–Friesian and Aberdeen–Angus cattle occasionally appears when it is positively known that all the progenitors have been black as far back as there is any record. Since red is recessive to black it is perfectly understandable that this color can be handed on from generation to generation by animals which do not themselves exhibit the undersirable character. In the same way, more serious defects, such as sterility, constitutional weaknesses, and imperfections in color and conformation, are being multiplied and carried on, and the breeder can only stand by helpless and see them appear from time to time in spite of anything he can do, unless he is willing to resort to the drastic procedure of a more intense system of inbreeding than has ever before been advocated. This will be discussed later.

Homozygosity not characteristic of best development.—On account of the great complexity of the interacting factors which produce the largest growth and greatest productiveness, it is practically impossible to produce the best animals of any breed and at the same time have their good qualities homozygous, that is, fixed in such a way that those individuals will breed true. In so far as they are fixed and breed true, they tend to be less vigorous, and this is the reason why purebred livestock often fails to show any decided superiority in comparison with the best grade animals.

The unquestioned value of registered livestock is due not so much to their own productiveness as to the concentration of good heredity in practically all the members of the breed. Their greatest value is generally utilized by crossbreeding or by grading. In this way the greater heterozygosity makes possible a more rapid growth and a better opportunity for their good qualities to be expressed.

Grading.—On account of the comparitively small number of purebred animals, the greatest opportunity for improvement in livestock at the present time lies in a more general use of animals of good breeding upon common stock, rather than in a further advance in the qualities of the purebred animals themselves. The practice of using carefully bred sires with nondescript animals of indiscriminate breeding is called grading-up. The opportunity for increased production in this way has been well demonstrated by Lippincott at the Kansas Station. Purebred White Leghorn, Barred Plymouth Rock, and White Orpington cockerels were used for three generations with three separate pens, starting with a mixed lot of mongrel farm hens bought from a poultry packing house. Their breeding had apparently received no attention whatever, as they were extremely varied in color and conformation. In three generations the color and other plumage characters were brought very close to the type of the breed used in the males, as shown

in Fig. 218. Compared with the original hens, the conformation was brought to a fairly high degree of uniformity, and the egg yield of the two lots bred to the sires from high-laying breeds was notably increased.

Graded poultry.—Comparing their production in the third graded generation with the averages for pure-bred hens of the same breeds, in flocks which have been directly selected for high egg production and entered in laying contests as given in Table XLVII, we see that the grades are certainly no less productive. On account of differences in location and probably in management, a strict comparison is not possible. In uniformity, in size and color of the eggs, the grades would probably not stand

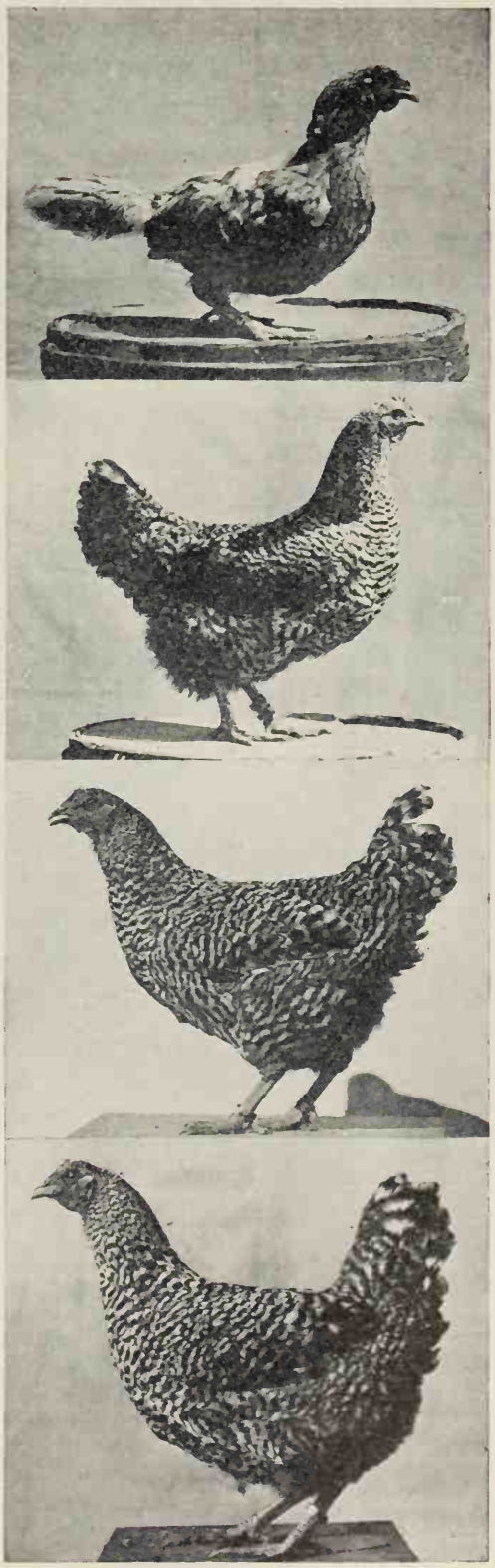


FIG. 218.—The result of three generations of grading by the use of Barred Plymouth Rock cockerels from high-producing families. From top to bottom: a mongrel hen that laid 100 eggs in her first year and the offspring of three successive matings, whose first year records are 182, 208, and 248 eggs, respectively. (After Lippincott in Kansas A. E. S. Bull. 223.)

TABLE XLVII

THE FIRST YEAR EGG PRODUCTION OF MONGRELS, AND FIRST, SECOND AND THIRD GENERATION GRADES COMPARED TO THE AVERAGE EGG YIELD OF SELECTED FLOCKS FROM THE SAME BREEDS

Data for Grades from Lippincott, in Kansas A. E. S. Bull. 223

Breed	Mongrels	First Generation Grades	Second Generation Grades	Third Generation Grades	Storrs Contest Average 4 Years 1912–1915	National Contest Mt. Grove, Mo. Average 4 Years 1912–1915
White Leghorn...	75	166	197	198	162	156
Plymouth Rock..	105	135	166	207	145	146

as high as the selected breeds. Yet in total number of eggs laid, these hens, which are only three generations removed from mongrels, are, if anything, somewhat superior to purebreds which have been directly selected for egg-laying capacity.

In the course of the grading-up, the pullets were selected on the basis of vigor and similarity to the breed of their sires. The egg records of their dams, however, were not consulted. Different males of the same breed were used with each lot in the successive generations. They were purchased from various sources, being chosen, as far as possible, from an egg-production standpoint. The egg records of their dams were known in most cases, as well as the records of their grand-dams on the male side. These records were uniformly high. As given by the poultrymen that bred them, they ranged from 200 to 285 eggs as individual yearly records. Among the third-generation grades there were fourteen individuals with records above 200, going as high as 262 eggs. A pen of mongrel hens was carried along by using cockerels of similar unknown breeding. Although the general average egg production was increased in the second generation, there were no individuals in any of the mongrel pens which laid over 200 eggs.

It would probably not be difficult to find purebred White Leghorn and Barred Plymouth Rock flocks that would average a somewhat higher egg record than these grades. Yet, if it is possible to take fowls which have received no attention whatever as to egg-laying capacity, and, by breeding them three successive times to standard bred males, with no selection on the female side, other than for vigor, get results that compare favorably with purebreds which have been specifically selected for egg yield, it shows that there is something decidedly lacking in the control over the heredity which the breeders now have. Apparently, whatever is gained by concentrating heredity in particular directions is more or less counteracted by loss in constitutional vigor due to the close breeding which is unavoidable. No matter how exceptional an animal may be in having an accumulation of particular qualities, unless that individual also has the vitality to withstand unfavorable conditions and to resist disease, and has the capacity to consume large quantities of food, all qualities which are summed up in the one word vigor, it can not produce exceptional results.

The mixed breeding of farm-raised fowls brings about a high degree of genetic diversity. Their egg production is only mediocre, but when they are bred to individuals which come from stock that has been specifically selected for laying ability, the good qualities of the purebreeds are given a good chance of finding expression when helped by the vigor resulting from the crossbreeding. There can be no doubt, however, that the greater production of the three-times up-graded mongrels, in comparison to the stock from which they came, raised under equal conditions, is due in a large measure to the purebred males, which were selected from high egg-producing flocks.

Since there is evidence, given by Pearl, that some of the factors for high egg production are carried in the sex chromosome, and because hens, being heterozygous for sex, receive this sex chromosome only from the male, it is possible that the use of purebred males for grading-up purposes is some-

what more effective in poultry than with other animals. On the other hand, the term "purebred," as applied to poultry, does not have the meaning that it has with the larger farm animals. No system of registry has been found to be practicable with such small and rapidly breeding animals, and it is to be expected that registered animals receive more care in their breeding than those which are not registered.

Grading with Shorthorns.—Practical demonstrations of the value of purebred livestock in improving the size, quality, and productiveness of farm-bred horses, beef and dairy cattle, sheep, and swine are plentiful, but no exact data are available to show the actual improvement brought about or to compare the grades with the purebreds. Probably the most extensive demonstration of grading-up the larger animals in recent years was started by W. R. Nelson at the Sni-a-bar Farms at Grain Valley, Missouri. Two hundred ordinary, small, mixed-bred farm cows were purchased at the stockyards and bred to registered Shorthorn bulls. Three generations of such matings have brought about a marked increase in the size and finish of the resulting animals, with a noticeable improvement in the quality of the dressed meat. In 1922, the calves from the cows bred to common bulls were appraised by commission men at $22 a head. The first and second generation calves, after the purebred bulls were used, were valued at $33 and $40 respectively. Fat steers of the same age and condition, from the first, second, and third crosses, were considered by the same authorities to be worth on the average $100, $115, and $125, respectively. While the valuations are merely approximations, they show in a general way the steady improvement that has been made.

Prepotency.—The outcome of a grading-up process of this kind depends upon the genetic constitution of the sires used. It is of the greatest importance that they have the ability to transmit their own good qualities to all of their offspring. Many individuals, and certain breeds in general,

have this power of passing their own characters on to their progeny, to the almost total exclusion of the characters of the animals to which they are mated. This capacity for obliterating undesirable traits is called **prepotency,** and is a faculty that is very much desired in all breeding stock. Prepotency is highly variable and difficult to establish in an outstanding degree, so that to many breeders it carries an element of mystery. There are many unproved assumptions in regard to prepotency. It is generally believed that it is a characteristic of an animal as a whole and is closely related to sex and vigor. A virile, masculine type in the male is thought to be an indication of general prepotency. Vigor is always desirable, but is not associated with prepotency in particular characters. Neither is there any foundation for the belief that prepotency in certain characters, such as color, is correlated with prepotency in others. As Wright [1] states, experiments fully substantiate these statements:

A white-faced red Hereford cow with normal horns produces polled, white-faced, black calves when bred to a polled, black Aberdeen–Angus bull. An Aberdeen–Angus cow produces the same kind of calf when bred to a Hereford bull. Evidently prepotency lies neither in the sex, the breed, nor the individual, but in the characteristics, polled head, black color (where there is any color besides white), and white face.

Somewhat similarly, a cross made in either way between an Aberdeen–Angus and a white Shorthorn produces polled blue-roan calves. Polled head and black color are prepotent, as before, but prepotency is lacking as regards the third pair of opposed characteristics, the solid color of the Aberdeen–Angus and the nearly solid white of the Shorthorn.

It is not the whole story, however, to say that certain characteristics are always prepotent. If in the case above, the polled, blue-roan Shorthorn–Angus crossbreds are bred back to a white Shorthorn, only half the calves will be polled, the rest having good horns, and only half will be black in the colored parts of the coat (that is, they will be blue-roan or white with black ears), the rest being red-roans and whites with red ears. Thus, the characters which were fully prepotent in the purebred cease to be

[1] From United States Dept. Agr. Bull. 905.

so in the crossbred. The difficulty is that the crossbred produces more than one kind of reproductive cells. In the present case, half of the reproductive cells transmit the polled condition and half transmit horns; half transmit black and half transmit red; half transmit the tendency to develop color in the entire coat, as in the Aberdeen–Angus, and half transmit the highly reduced condition of color, as in the white Shorthorn. Moreover, the

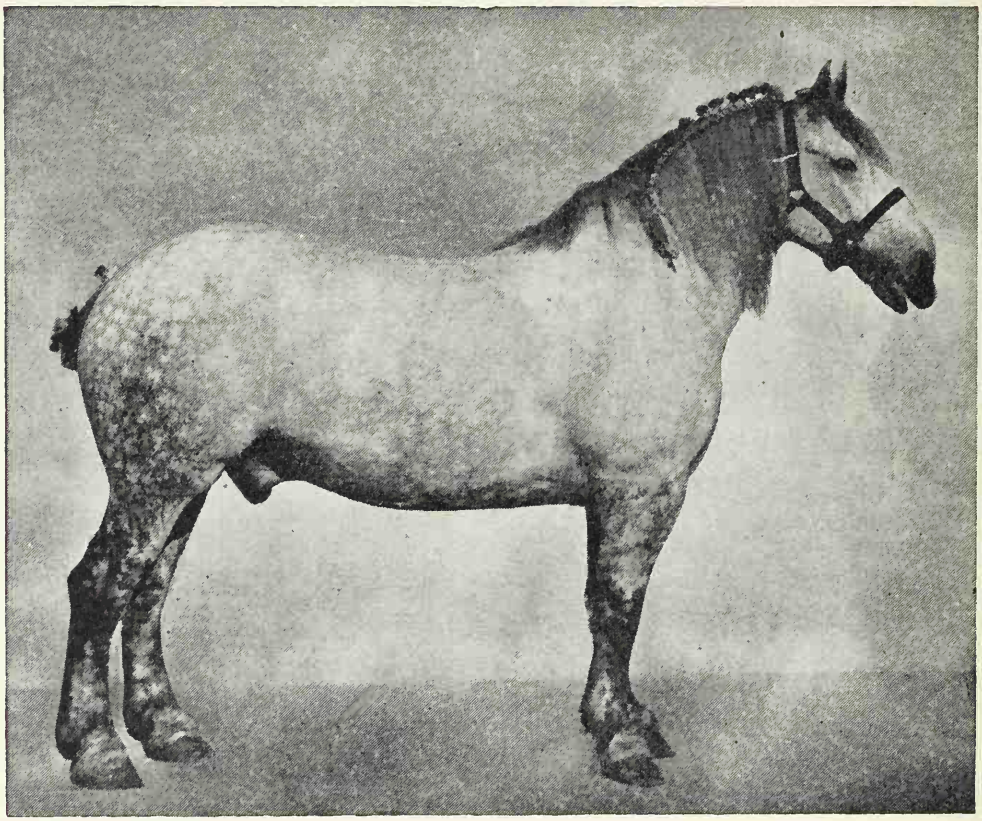


FIG. 219.—"Big Jim," the product of a purebred Percheron stallion mated with a grade mare of the same breed, showing the value of concentrating desirable qualities by close breeding in purebred livestock. (After Sanders and Dinsmore in "A History of the Percheron Horse," courtesy of Sanders Publishing Co.)

representatives of the three sets of opposed characters are shuffled up and sorted out into the reproductive cells independently of one another. Some of the reproductive cells transmit the combination polled, solid color and black, others polled, solid color and red, and so on through the eight possible combinations.

In this illustration we have used characteristics which have already been discussed as examples of simple Mendelian heredity. Most characteristics probably depend on a much larger number

of hereditary units, but, nevertheless, the nature of prepotency is believed to be essentially the same. So far as there is prepotency, it is a property of characteristics (or really of the hereditary units back of the characteristics), not of individuals, breeds, or sexes, and whatever the characteristic, there can be no prepotency unless the individual produces only one kind of reproductive cell so far as it is concerned.

Prepotency is primarily a matter of dominance and homozygosity of the factors which determine the expression of the visible characters in which prepotency is shown. The hope of the breeder is to produce a prepotent animal that will impress his characteristics, however mated, on all his progeny. This is practically an impossibility, since as much depends upon the animals with which he is mated being recessive, in those qualities for which he is dominant, as upon his own composition. Furthermore, there is evidence that prepotency depends upon the proper relation of all important factors with each other, as the same factors which show dominance in some individuals are not always as fully expressed in others.

Purebred livestock not always the most productive.—Since the value of purebred livestock is quickly shown in grading-up experiments with scrub stock, it is generally assumed that there is a continued improvement with each successive back cross. This assumption is not fully supported by the facts. Neither is the universal superiority of purebred livestock over the better classes of grade stock for strictly production purposes proved beyond question. That the most carefully bred animals are not always the most valuable for practical uses is indicated by the widespread practice of crossbreeding.

Crossbreeding.—In spite of their handicap of having no value for breeding purposes, crossbred animals are commonly seen. Their sturdiness, rapid growth, and economy of gains commend them to the general farmer who is producing for the market. The fact that the first crossing of two well-established breeds of animals is often beneficial in bringing about larger numbers of young, greater vigor, and hardiness

is well known. Bringing together the valuable market features of the wool and mutton breeds of sheep, of somewhat different types of pigs, and the important qualities of the different breeds of beef cattle is a widespread practice, and for good reasons.

However, there are very few exact data upon which to base a fair comparison of purebred and crossbred animals on a production basis. Farm practice indicates the value placed upon crossing for particular purposes. In Scotland, the black Galloway and Aberdeen-Angus breeds have been extensively crossed with white Shorthorns for a hundred years. This combination has a distinctive blue-gray color, which for this reason has long been associated with high

FIG. 220.—The first-generation cross of black Galloway cows with a white Shorthorn bull. Note the uniformity in color, size, and conformation. (After Lloyd-Jones and Evvard in Iowa A. E. S. Research Bull. 30.)

quality in meat animals. A large number of Galloway by Shorthorn crossbreds were raised at the Iowa Station and, as reported by Lloyd-Jones and Evvard, possessed high merit from the market standpoint and seemed to justify the high esteem in which these cattle were held. (See Fig. 220.)

Crossbred sheep.—In general, crossbred animals are intermediate as compared with their parental races. Thus, crosses between two breeds specialized in different directions are commonly more suitable for general purposes. Russell, at the Oklahoma Station, gives the results from three hybrids between wool and mutton breeds of sheep in which the weight of body and wool clip were intermediate, but the

TABLE XLVIII

WEIGHT OF BODY, PRODUCTION OF WOOL AND MARKET VALUE OF WOOL OF THREE BREEDS OF SHEEP AND FIRST GENERATION CROSSES BETWEEN THEM

Data from Russell, in Oklahoma A. E. S. Bull. 126

Breeds and Crossbreds	Number of Animals	Average Weight of Body, Pounds	Number of Fleeces	Average Weight of Fleece, Pounds	Price per Pound, Cents	Average Value of Fleece, Dollars
Dorset	34	166	181	7.2	17.25	1.24
Shropshire	14	136	66	9.5	17.25	1.64
Merino	24	116	83	16.3	10.00	1.63
Dorset × Shropshire	16	148	30	10.0	17.25	1.72
Dorset × Merino	13	143	24	12.0	15.25	1.83
Shropshire × Merino	..	...	1	15.0	15.25	2.29

FIG. 221.—Calves of the second generation from some of the crossbred cows in Fig. 220, showing the non-uniformity in color. (After Lloyd-Jones and Evvard in Iowa A. E. S. Research Bull. 30.)

total market value of the wool was increased as shown in Table XLVIII. J. M. Jones, at the Texas Station, gives averages for five crossbred combinations of sheep, based upon fairly reliable numbers, which show a marked increase in weight and market value in practically every case over one parental breed. On the other hand, Ritzman and Davenport compare the first-generation crosses between Southdown and Rambouillet sheep and find that they are

intermediate only in height. In other dimensions and in weight, the crossbred animals are below the average of the two parental races, showing that not all combinations give an increase in size.

Crossing swine breeds.—The animals with which crossing is most extensively practiced are swine. From the disastrous results of inbreeding obtained at the Delaware Station and previously discussed in Chapter XII, it is easy to see why crossing is favored. In a quick-maturing animal of this kind, it is highly important to secure as large a number of young as is consistent with full vigor and quick

FIG. 222.—First-generation cross-bred ewes of Cheviot by Delaine Merino. (After Severson, courtesy of the Pennsylvania State Agr. College.)

early growth. That fertility is increased and mortality decreased by crossing swine is well shown in the data furnished by Casement in Table XLIX.

Poultry crosses.—The breeds of poultry are so many and varied that there is little object in crossing to produce a new type of fowl as a first-generation product, as nearly all requirements can be met in some already existing breed. Moreover, this class of livestock is so extensively intercrossed that there is not so much to be gained by crossing as in some of the other animals. Strains which are closely selected to type give a greater increase in size and productiveness when crossbred. First-generation combinations of the light, egg-laying, Mediterranean breeds with the heavier-

TABLE XLIX

MORTALITY AMONG PUREBRED AND CROSSBRED PIGS FROM SOWS OF THE SAME BREEDS

Data from Casement, in *Breeder's Gazette*

Breed	Number of Litters	Average Number of Pigs per Litter	Percent Dead at Birth	Percent Alive at 105 Days	Average Number of Pigs Raised per Sow
Duroc Jersey sows	18	9.4	10.6	42.9	3.6
Poland China sows	7	7.7	20.0	37.2	2.3
Duroc Jersey sows crossbred by Yorkshire	5	12.4	3.5	70.0	7.6
Poland China sows crossbred by Yorkshire	3	9.3			

bodied fowls are sometimes produced to give a greater weight together with high egg-laying capacity.

Separating the sexes of poultry by color characters.—In commercial egg production it frequently does not pay

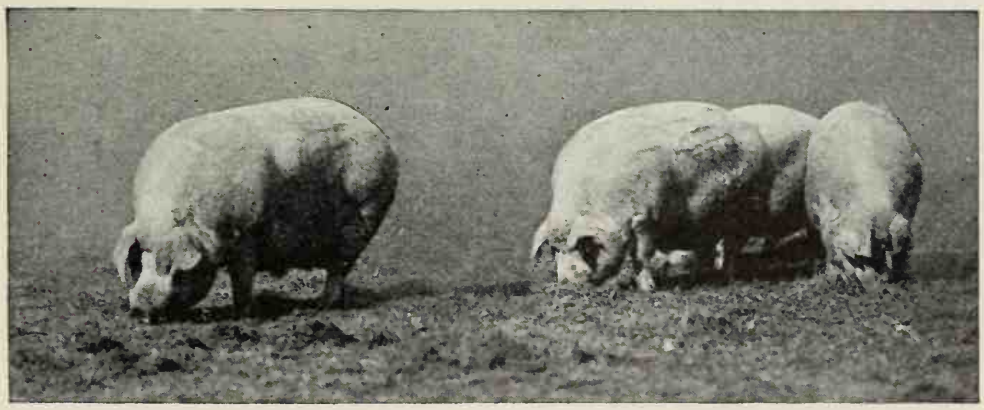


FIG. 223.—First-generation cross of Chester White by Poland-China. (Courtesy, Illinois Agr. Exp. Station.)

to raise the cockerels, provided that they can be eliminated immediately after hatching. Sex-linked characters can be applied to poultry in such a way that the sexes can be identified at hatching time by the use of suitable sex-linked color characters. Since the females of birds have the

heterozygous sex chromosome pair, whenever a female having a dominant sex-linked color is mated with a male having the recessive allelomorph, the result is the criss-cross inheritance, such that the male offspring have the same color as their dams and the females are colored like their sires. When certain characters are used, the differences are so distinct in the newly hatched chicks that they can be readily separated. The barred feathers of the Plymouth Rock and Dominique breeds are due to a sex-linked factor, and when females having this pattern are mated with buff, red, or black males of any breed the result is that the males are all barred and the females not barred. This result ensues only when the birds used are purebred for the color factors employed. Standard-bred flocks are sometimes segregating for color and plumage pattern. It is not unusual to get an occasional black individual from only barred pens. Such individuals are always females and the fault lies with the males used. Since the females have only one factor for barring, they can not carry any recessive sex-linked characters, such as the solid color, due to the absence of the barring factor, without showing it on their own feathers. The males, however, having the two sex chromosomes, may carry recessive sex-linked factors. Other color characters can be used to separate the sexes at hatching time. All varieties with the Columbian pattern, such as Columbian Rocks, Wyandottes, Leghorns, and Light Brahmas, can be crossed with buff males, and the resulting White or Columbian pattern chicks will all be males and the buff chicks females. Since there is a buff variety in every breed which has a Columbian variation, color combinations can be made without going out of the breed, if desired. Silver Campines, Silver-Penciled and Silver-Spangled Hamburgs, and others have corresponding gold varieties which may be used with them in the same way to separate the sexes at hatching time.

Although the types available for use in this way do not include all of the most popular breeds of farm fowls, so many

are available that commercial hatcheries can supply chicks of either sex desired, to meet nearly all demands as to type. It is obviously impossible to use the males produced in this way for further crossing, since they are all heterozygous for plumage color. The females, on the other hand, transmit only one color combination and, where they come from

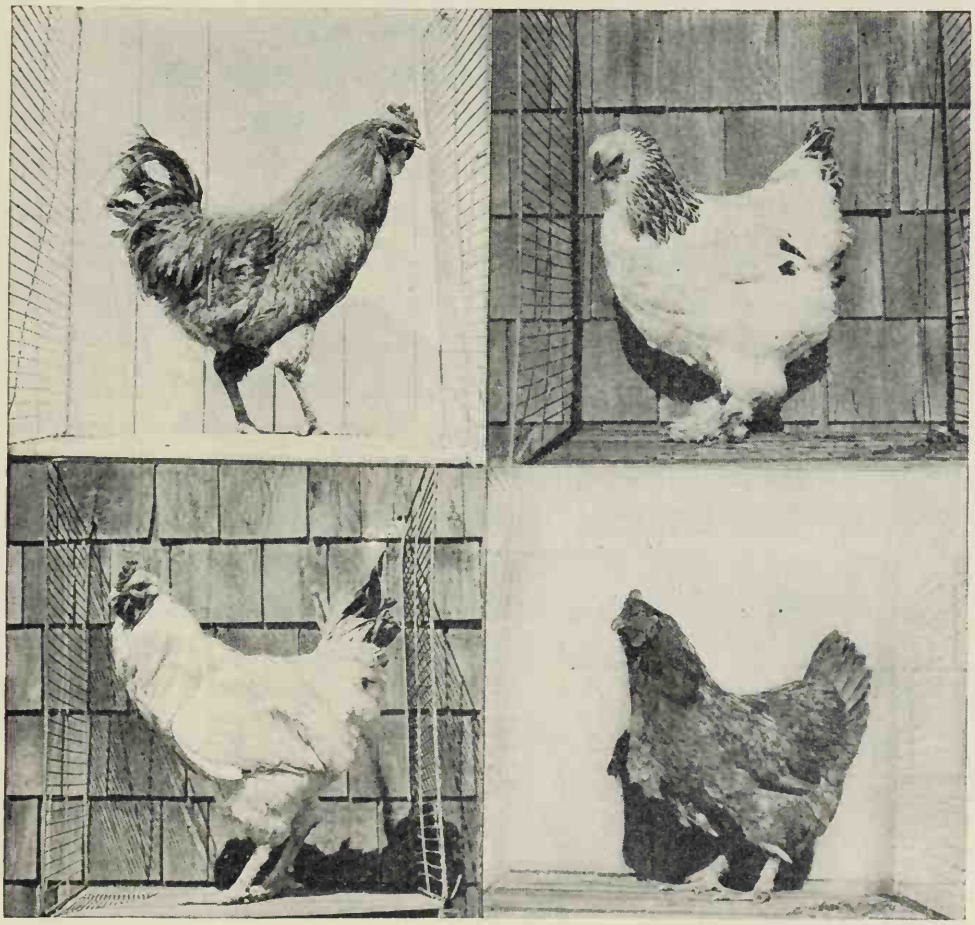


FIG. 224.—Buff male and Columbian pattern female give white male and buff female chicks which can be separated at hatching. (From Dunn, courtesy of Conn. Agr. College.)

crosses within the same variety, can be used for breeding. However, this method of sex identification is best used with a systematic production of first-generation hybrids, where highly selected purebred strains are produced for the primary purpose of crossing. The only objection to this method is the fact that the color patterns of crossbreds

are often less clearly marked than in purebreds. When barred fowls are crossed with non-barred races, the barring is not so clear-cut as in selected barred breeds. The loss in this respect is of minor importance considering the value to be gained by crossing.

Crossing for special purposes.—Gowen, at the Maine Station, finds that first-generation crosses between the dairy and beef breeds have the milk yield very largely suppressed, and that the meat-making qualities are not suffiently improved to make this combination of any value as a dual-purpose type. However, sires of the beef breeds are used with dairy cows for the special purpose of increasing the market value of calves which are not wanted for milking. Dorset sheep are particularly valued for their propensity to produce early spring lambs. Rams of this breed are frequently used to produce crossbred ewes, which have this tendency more highly developed than the general mutton breeds. Aside from these special applications of crossbreeding, there is no object in employing this practice unless there is a sufficient increase in size, quality, early maturity, or other valuable market qualities to justify the maintenance of breeding animals largely for the purpose of producing the crosses.

The importance of crossbreeding to the livestock industry lies in the fact that no one breed can have the best development of all desirable features. If it were otherwise, there would be no need for more than one breed in each kind of farm animals. The many different breeds that now exist have been developed in response to particular demands. Some types are noted for small bone and large proportion of meat, but are inclined to be weak, unprolific of young, and subject to loss by disease and exposure. Others, which are large and rugged, are often slow-growing and lacking in quality. As long as variation occurs, there will be many different varieties of domesticated animals to suit different needs. Crossing among these tends to bring together at once, but for one generation only, more of the valuable

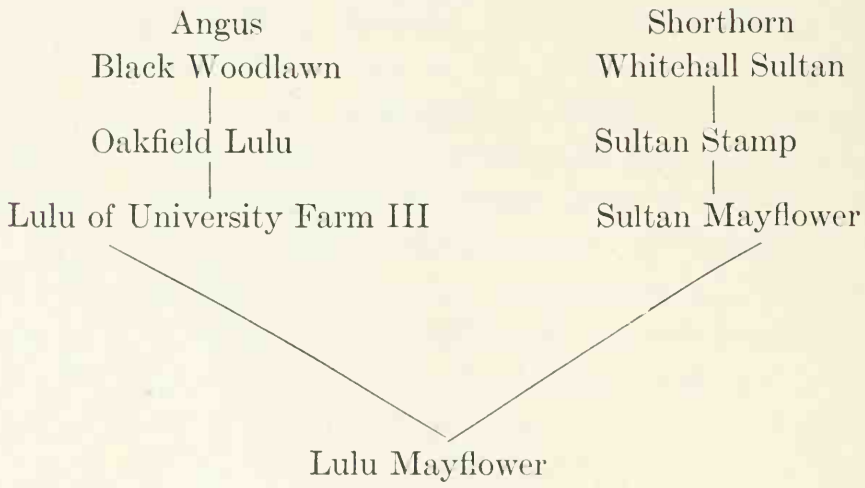
qualities of both parental types than it is possible to get together in any other way, and at the same time weaknesses and infertility are very largely suppressed. The result is that rapid-growing animals of high quality are produced at the least cost for feed. This bringing together of the best of both parents is the basis for understanding the phenomenon of hybrid vigor in increasing size and rapidity of growth above that shown by their parents. Crossing in itself carries no mysterious stimulus to greater size and vigor, just as, conversely, inbreeding does not reduce size and vigor because such a system of mating is inherently harmful.

Value of crosses can not be told in advance.—Not all crossbred combinations give the fine results that some do, and it is never safe to predict the outcome of any particular cross by judging from the appearance of the animals used. When the cross is once tested and proven good, however, a similar combination can be made repeatedly by using breeding stock from the same sources, with reasonable surety of getting equally good results each time. It should be fully appreciated that the whole value of crossing lies in the good qualities which are present in the stocks brought together. Crossing is not a means of escaping the consequences of blunders in breeding. One can not expect to get any more out of a cross than is put into it. However, there are many good points in different breeds which have never been fully brought out. This is particularly true when the families have been closely inbred. The right hybrid combination allows their potentialities to be expressed more completely, and the result is often exceptionally good. It is in this way that many of the champions of the livestock expositions have been produced. Nevertheless, it can not be too often restated that it is the good heredity carefully concentrated in purebred livestock that makes crossing a paying proposition.

Good qualities of crossbreds come from purebred livestock.—The value to be derived from crossing comes from

the uniform excellence of the parent stocks brought about by the systematic selection which the pedigree record system has made possible. There is not much to be gained by crossing animals that have not been carefully selected. Such animals are themselves hybrids, and crossing them with each other does not add anything of value. By recombination, their weak points, which are masked by their previous crossing, are brought to light. Uniform progeny are produced only when the parental races are fixed in their particular type and breed true, and it is only when they are from separate and different lines of descent that decidedly beneficial results from crossing can be expected. In the common practice of crossing, it is only when a purebred sire is used that results worth noticing are regularly secured, and when the dams are purebred and from unrelated stock the best results may be expected.

One has only to look at the pedigree of Lulu Mayflower, the 1921 Grand Champion at the International Livestock Exposition, to see where she gets her right to stand among the first.



Both grandparental sires are famous representatives of the Aberdeen–Angus and Shorthorn breeds. Themselves grand champions, they have been in part the source of many others. Moreover, numerous progeny from the same dam

and grand-dam as Lulu Mayflower have won high honors as pure representatives of their breed.

Registered livestock has been rigidly selected towards definite standards. Each breed has certain qualities which make it valued above all others. They have these qualities built up to a higher degree than is possessed by any large

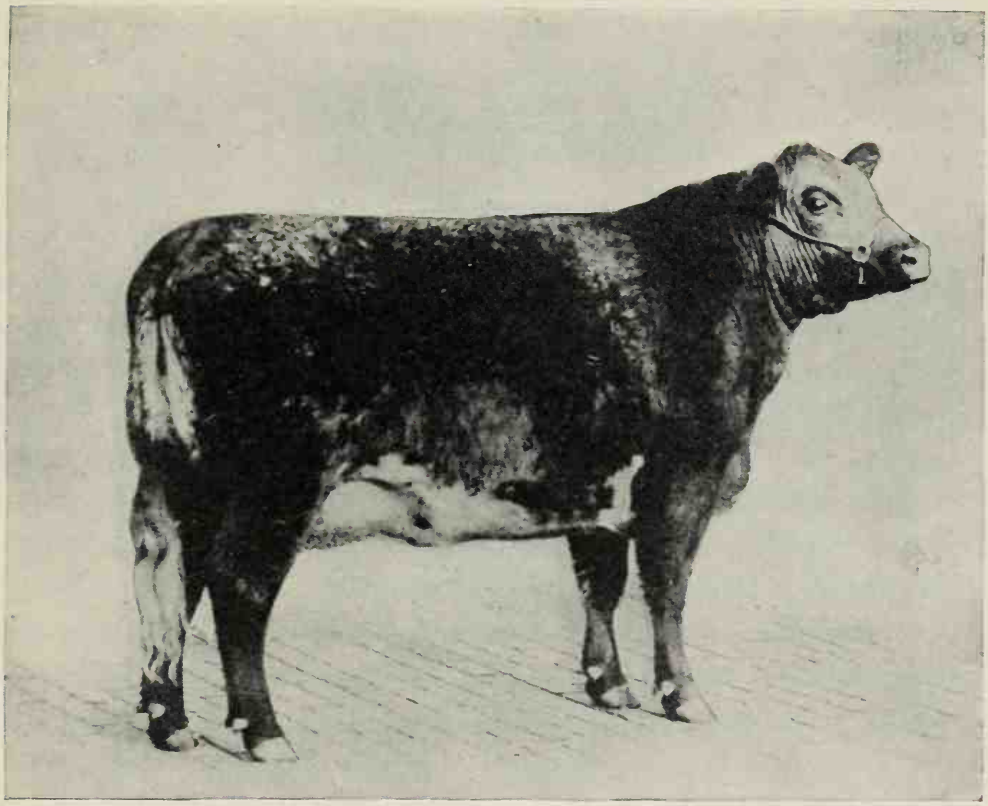


FIG. 225.—"Lulu Mayflower," grand champion at the International Livestock Exposition in 1921, a first-generation cross between a purebred Aberdeen Angus cow and a purebred Shorthorn bull. (Raised by the California A. E. S., photograph furnished by True.)

number of animals resulting from any other system of breeding. Their pedigree record insures that they will come fairly true to that type. But purebreds, when compared with the better classes of non-pedigreed livestock, are often somewhat lacking in vigor, rapidity of growth, and fecundity, three very important considerations from the standpoint of the man on the farm who is making his

living by producing meat and milk, wool and eggs. The very qualities which close mating unavoidably brings in are counteracted by crossing. Prolificacy, hardiness, and rapid growth are the outstanding features of crossbreds. In hybrid vigor there is a very real help towards increased production. Why not use it?

Objections to crossbreeding.—There are several reasons why crossing is not more generally practiced than it is. In the first place, the breeders and sellers of purebred livestock discourage crossing. Nearly all writers on animal breeding see so clearly the absolute necessity of maintaining the invaluable pure breeds of livestock which we now have, and making them still better, that they minimize the real benefit to be derived from crossing the breeds for production purposes. They hesitate to say anything which to them looks like breaking down that system which has had everything to do with building up the livestock industry to the high plane on which it exists to-day. The time is at hand when a broader viewpoint should be taken. The foundation work of creating the breeds has been done and done well, but there is still a great deal lacking.

The 1920 census reports the percentages of purebred livestock in this country as follows: horses, 0.6 percent; cattle, 3.0; sheep, 1.3; swine, 3.5. Less than 4 percent of the livestock in the country is purebred and registered. According to Wentworth, little more than one-half of all animals have sufficient characteristics of the recognized breeds to be classed as grades from registered stock. It is not wholly because of the initial cost of purebred stock that this state of affairs exists. Many would buy registered animals if they were absolutely convinced that they could increase their production profitably by so doing.

A more general appreciation of the real value which lies in crossing, with a full knowledge of its limitations, would do a great deal towards increasing the demand for animals of proved breeding. This would greatly increase the total number of purebred animals in the country and at

once dispose of the argument, often brought up, that crossbreeding will reduce the opportunity for selecting and still further improving the breeds. There is no reason why a widespread practice of crossbreeding should interfere with this important work. It will rather increase the incentive and widen the means for bringing it about. Instead of a few purebred families in a community, many will be needed to supply the material to produce the crosses.

Crossbred animals themselves are practically worthless for further breeding.—The reason for this must be thoroughly understood. The weaknesses and undesirable qualities which are overcome by crossing are certain to reappear in the offspring. For example, many of the progeny of a crossbred wool and mutton sheep will have the inferior fiber and light clip of one parental race together with the lanky body and coarse carcass of the other. The animals will not be uniform in size or shape; nearly all will be less vigorous than their hybrid parents and some may show decided abnormalities. The continued breeding of Berkshire–Duroc Jersey or Poland China–Chester White crosses may easily bring forth four-legged creatures that are inferior in size and vigor to the poorest specimens in either pure breed. The experience of practical breeders and livestock feeders everywhere and the results of controlled laboratory experiments with animals and plants have not left a single doubt that the further mating of offspring resulting from wide crosses is unprofitable. Occasionally an exceptionally good individual will stand out, but the general run will be decidedly undesirable.

The necessity of maintaining breeding stock primarily for the production of crosses presents many difficulties, increases the expense, and is the only justifiable objection which can be held against crossbred animals for market purposes. This is a limitation that has not prevented the mule from being widely used. Farming is more and more becoming specialized. Many animals are fed which have been bred elsewhere. When it is noted that the best repre-

sentatives of the breeds are never used for crossing because they are too valuable for continuing their kind, the fact that many crossbreds compare favorably with the foremost examples of any breed is still more significant. However, a method may be theoretically sound and at the same time not practicable under existing economic conditions. The necessity of more intensive methods justifies increased attention to the utilization of hybrid vigor.

Crossbreeding gives a more complete control over heredity.—If animal breeding were based primarily upon the

FIG. 226.—First-generation cross of Shropshire and Merino. First-prize crossbred yearling ewes at the International Livestock Exposition in 1917. (After Tomhave in Pennsylvania A. E. S. Bull. 163.)

utilization of first-generation crosses for strictly production purposes, this practice would permit a more complete control over hereditary transmission than is now obtained. As it is, effort is now constantly put forth to maintain maximum vigor. Together with this, it is desired that this large growth be transmitted uniformly to all the progeny. From the way in which the hereditary mechanism works, this is an impossibility. Full vigor together with the highest expression of desirable characters is only obtained in heterozygous combinations. Theoretically, it is possible to have the same factors which bring about maximum

growth in a homozygous and therefore true-breeding condition; but in actual practice it is so difficult to bring about this condition that working towards that end is hardly worth while until better methods of genetic analysis and control over the hereditary process than are now known are worked out. In view of the fact that new characters are continually appearing and that market requirements are constantly changing, even if a uniform and stable breed were established, it is doubtful if it would have a very wide range of usefulness as a pure breed for any considerable length of time.

Since the same results can be secured just as surely and much more easily by a system of close breeding to fix desirable heredity, followed by crossing to bring about full size and vigor, it is a theoretically sound procedure to inbreed much more intensely than is now generally considered advisable. Most breeders stop close mating as soon as evidences of reduced size and weaknesses appear, counteracting any tendency in this direction by outcrossing. The necessity of bringing in new germplasm frequently for this purpose is one of the serious handicaps which the present system of breeding has to contend with.

Eliminating undesirable heredity by inbreeding.—Those who discontinue inbreeding and cross out of the family to counteract weaknesses which result from close mating stop just before the greatest good is accomplished. The very fact that undesirable traits appear is evidence that the stock is heterozygous and is carrying recessive weaknesses. One of the most common tendencies in closely bred animals is towards reduced fertility. Many forms of barrenness and sterility are hereditary and are not always due to reduced vigor, as is generally assumed. The only permanent remedy is intensive inbreeding of the closest kind until the particular undesirable tendencies are eliminated. In this connection it should be recalled that, at the Wistar Institute, Miss King has inbred rats by brother and sister mating for twenty-five generations with no loss in

fertility where systematic selection has been practiced. Wright obtained similar results with some characters in

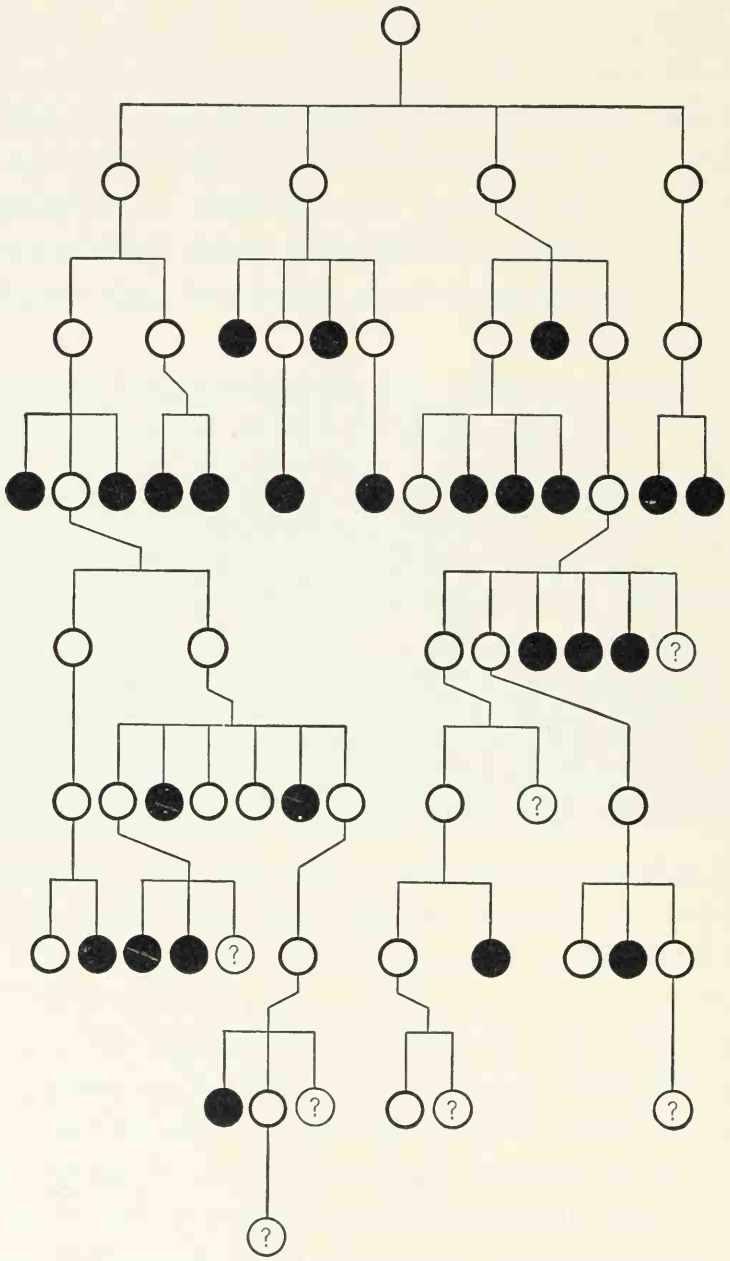


FIG. 227.—Inheritance of barrenness in the Duchess family of Shorthorns bred by Bates. Cows without offspring represented by solid black circles. (After Babcock and Clausen, courtesy of McGraw-Hill Book Co.)

certain families of guinea pigs that had been bred in the same way for twenty generations, but not with all. Domes-

tic animals will not keep up in vigor when inbred as intensively as this, but there is no reason why the hereditary factors necessary for full fertility can not be retained to give the best results when vigor is regained by crossing.

Good heredity more easily selected and fixed in inbred stock.—At the same time that sterility and other outstanding undesirable traits are eliminated, good qualities can be selected for, with a greater degree of certainty of holding them when secured, on account of the increasing uniformity and stability. How intensely inbreeding can be practiced depends upon the material worked with. Obviously, there are many serious objections to inbreeding animals so closely that their size and vigor are appreciably reduced. The cost of maintaining animals is so high that the expense of carrying along individuals which have little value in themselves, for the sole purpose of their future use as breeders, may easily be prohibitive. Moreover, the young of animals are so dependent upon their mothers for their first growth that the dams could be but very little lessened in size and constitutional strength without giving their offspring a handicap that they could not overcome with any amount of hybrid vigor brought in by cross mating. This objection would not apply so forcibly to the males, and there is every reason why sires should be selected on the basis of uniform transmission, which only results from homozygosity, rather than on account of large size and lusty vigor, qualities which are desirable in breeding stock only in so far as they are handed on.

The best system of livestock breeding must be a compromise between fixity of type and uniform transmission on the one hand and rapid growth and vigor on the other. Theoretically, the most desirable system, leaving out the matter of cost, would be based upon purebred registered animals which have been closely selected in inbred families so that their good qualities are fixed and permanent. The full expression of these good qualities would be obtained by the utilization of first-generation crosses between these

families, the crosses being made either within the breed or between different breeds, as the results obtained would indicate the best procedure. In fact this is the system that is being followed to a certain extent by purebred livestock growers as well as by farmers producing for the market. From the time that Thomas Bates united the two closely, but separately, bred Duchess and Princess families and produced some of the finest Shorthorns that had existed up to

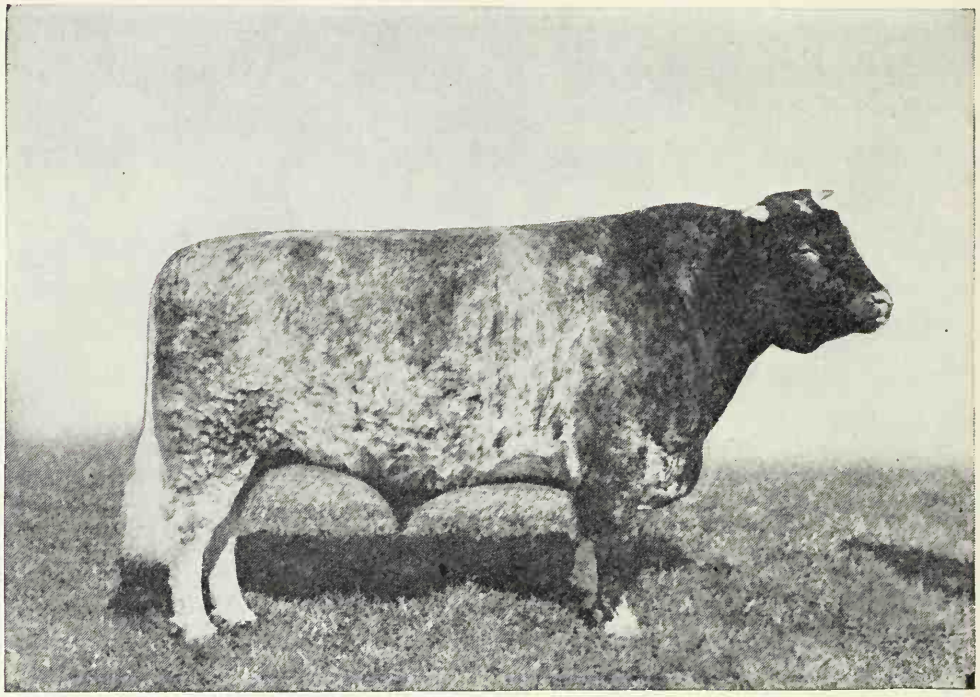


FIG. 228.—"Whitehall Marshall," a Shorthorn bull that scored higher than "Avondale" but was not so successful as a sire.

that time, many of the outstanding specimens of the breeds have resulted from the bringing together of different families each of which is closely inbred. Instead of being sent to the slaughter house, as they often should be, these heterozygous individuals are sold for large sums, and the purchasers frequently find that these splendid individuals are woefully lacking in ability to hand on their own valuable qualities. The cattle ranger, the shepherd, or the swine feeder who buys purebred sires of breeds of somewhat different type than the

dams with which they are used, to produce animals solely for the market, is following a system that is scientifically more sound than that of the breeders of registered livestock, who still base their selection largely upon appearances, relying upon skill and experience in judging, which can tell nothing as to the ability of the animal to transmit his own qualities.

Appearance not a reliable guide to breeding ability.—

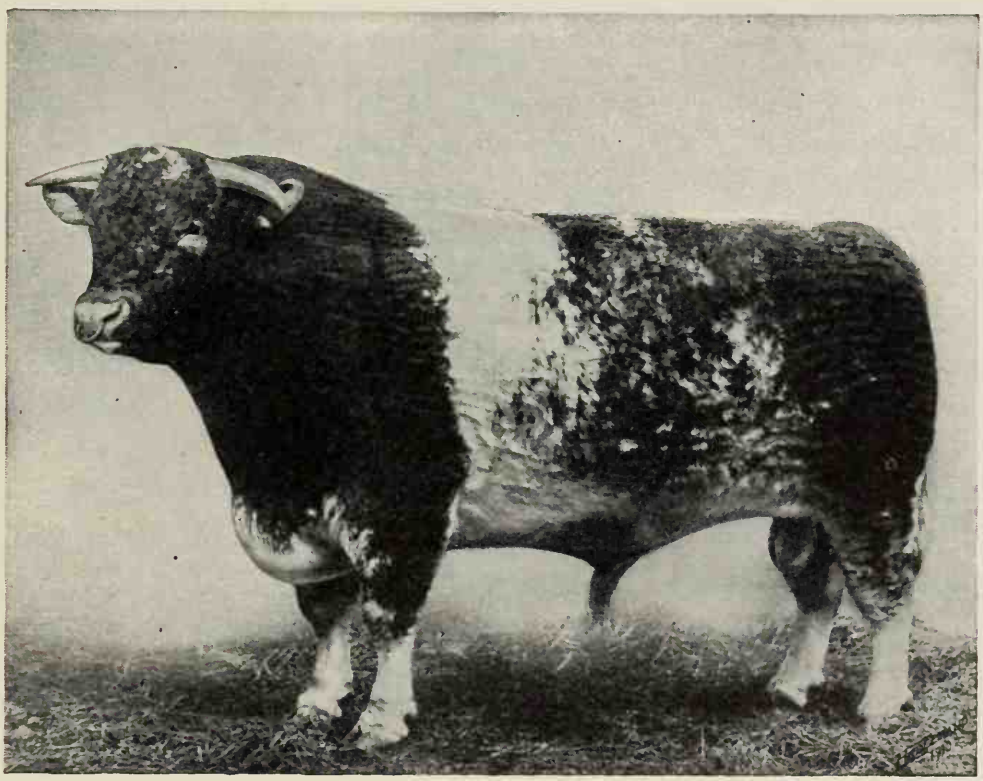


FIG. 229.—"Avondale," the leading Shorthorn sire in recent years, who stood fourth in the International Livestock Exposition in 1908.

For a good illustration of this well-known fact, let us turn again to the Shorthorns. At the International Livestock Exposition in 1908 there were four sons of Whitehall Sultan that stood first, second, third, and fourth in the aged class. The one that took the first prize, Whitehall King, turned out to be only a moderately good sire. The two that stood second and third proved to be somewhat better sires than the

first, but the one that was last of the four in the show ring was Avondale, who later proved to be the leading sire of the Shorthorn breed in recent years. Moreover, Matchless Dale, a son of Avondale, was another good sire that never took first place at any show but proved exceptionally successful as a producer of prize-winning steers.

Inbreeding as a process of purification.—Whether or not systematic crossing is relied upon to secure the best development, inbreeding can be used to a greater extent than is commonly recognized. Whenever marked tendencies to sterility and barrenness appear and other serious defects keep reappearing, the remedy is intensive close mating accompanied by rigid selection so as to eliminate the undesirable characters as quickly as possible. When these are gotten out, as shown by the fact that the surviving individuals no longer produce animals with the defects, different lines can be brought together and the original breed recreated and carried along by the same system of breeding as previously followed. Nothing of value is necessarily lost by inbreeding, and vigor can be restored in increased measure because of the hereditary weaknesses which have been weeded out. Selection in inbred families, carried out in this way, has a wide applicability, and while it is a drastic procedure it is far better than continued outcrossing which merely masks the weaknesses, increases them in numbers, and hands them on as a problem for the future to solve.

Selection in inbred families.—While the practical application of the system of selection in inbred families has yet to be fully demonstrated, it is based upon sound principles. It is the outcome of the epoch-making discovery of Mendel in regard to the alternative nature of inheritance, which, together with the germplasm theory of Weismann, led to a full appreciation of the fundamental distinction between variations which are somatic and transitory and those which are germinal and permanent. This knowledge, together with the demonstration by Morgan of the mechanism of

heredity, has for the first time led to a clear understanding of the full significance and importance of inbreeding. This has made possible a far greater control over heredity than has ever before been possible. The widespread application of these principles to both plant and animal breeding has possibilities of real practical improvement.

GLOSSARY

Acquired Character.—A change from the normal condition of the race in structure or function, brought about during the life of the individual.

Aleurone.—The outermost layer of the endosperm in cereals.

Allelomorph.—One of a pair of contrasted characters: one of the pair of factors determining the development of such characters, and occupying the same locus in homologous chromosomes.

Apogamy.—The formation of an individual without true sexual fusion.

Asexual Reproduction.—Any method of propagation that does not involve the fusion of gametes.

Atavism.—The appearance of ancestral characters in an individual.

Autosome.—Any chromosome other than the sex chromosome.

Biometry.—The branch of science dealing with the statistical investigation of organic differences.

Bos.—A genus of hollow-horned ruminants having simple horns in both sexes, typical of the family Bovidae and the sub-family Bovinae, including the oxen or cattle.

Breeding.—The art of improving animals and plants by hybridization and selection.

Bud Mutation.—A germinal change occurring in the very early history of a bud, such that the branch produced from it differs from the remainder of the plant.

Bud Sport.—A branch, flower, or fruit that differs germinally from the remainder of the plant.

Castrate.—To remove the reproductive glands.

Cell.—A protoplasmic body out of which organic tissues are built.

Character.—One of the many details of structure, form, substance, or function which make up an individual organism.

Chimera.—An association of tissues of different parental origin and germinal constitution in the same part of a plant.

Chromatin.—The substance of which the chromosomes are largely composed, so called on account of the readiness with which it becomes colored by certain dyes.

Chromosomes.—Minute structures composed largely of chromatin, having a more or less definite and characteristic size and shape at certain stages of development of the cell and a definite number for each species.

Cion.—A part of a plant, usually a short piece of a small branch, joined by grafting with another plant or part of a plant, the stock, for the purpose of producing a number of individuals that will grow or fruit alike.

Clone.—A group of individuals produced from a single original individual by some process of asexual reproduction, such as division, cuttings, etc., or parthenogenesis (when unaccompanied by any change in the chromosomes). In budded or grafted plants, part of the plant may belong to one clone and the other part to a different clone or to a variable lot of seedlings.

Crossing-over.—Exchange of factors between homologous chromosomes.

Cytology.—The study of cells, especially with regard to their internal structure.

Cytoplasm.—Cell protoplasm outside of the nucleus.

Dam.—A female parent, used with reference to mammals; in contrast to sire, the male parent.

Determiner.—*See* **Factor.**

Development.—The complete process of growth of an individual.

Dioecious Plants—Those having the two sexes on separate individuals.

Diploid.—The condition in which both members of a chromosome pair are present, the way in which the chromosomes usually occur in the somatic cells of the species; twice the gametic or haploid number.

Dominant.—A term applied to that member of an allelomorphic pair which has the quality of manifesting an effect wholly or partly to the exclusion of any effect from the other member; the opposite of recessive.

Drosophila.—A genus of flies, *D. melanogaster*—the pomace, or fruit fly.

Duplicate factors.—Two or more factors either of which alone produces the same result.

Egg.—The female germ cell; ovum.

Emasculation.—The removal of the anthers from a flower in the bud stage, before pollen is shed.

Embryology.—The study of the early development of the egg leading to the formation of an embryo.

Endosperm.—The substance stored in a seed, for the early nourishment of the embryo, to which it is adjacent.

Environment.—The sum of the influences which have their origin outside of the body.

Factor.—A unit of inheritance; a transmissible element of the genotype, the presence of which makes possible a specific reaction or the development of a particular character of the individual which possesses that genotype; a determiner, or gene.

Fecundity.—The potential reproductive capacity of individuals; the ability to produce mature ova and sperm.

Fertility.—Ability to produce normal, living young; the opposite of sterility.

Fertilization.—The union of male and female sex cells.

Gamete.—A mature male or female reproductive cell, usually containing the haploid number of chromosomes.

Gene.—*See* **Factor.**

Genotype.—A group of individuals all of which are alike with respect to their hereditary factors; the constitution of an organism with respect to the hereditary factors of which it is made up; the sum of all the genes of an organism.

Genus.—An arbitrary group in the systematic classification of plants and animals, ranking next above the species, and containing one or more species possessing certain structural characters different from those of other genera.

Germ Cells.—Cells specialized for sexual reproduction; the ova and spermatozoa in animals, the egg cells and pollen grains in plants.

Germplasm.—That part of the cell protoplasm which is the material basis of heredity and is transferred from one generation to another; in contrast to somatoplasm.

Gonads.—The glands that produce the reproductive cells.

Graft Hybrid.—A shoot or plant which has been produced by grafting one kind of plant upon another, and the characters of which are intermediate with respect to the two components.

Gynandromorph.—An animal in which one part exhibits female characters and the other part, male characters.

Haploid.—The condition in which only one member of each chromosome pair is present, usually occurring only in the gametes; one-half the somatic or diploid number.

Hermaphrodite.—Having both sexes in the same individual.

Heterosis.—The increased growth stimulus often exhibited by a hybrid.

Heterozygote.—A zygote resulting from the fusion of unlike gametes; an individual whose allelomorphic pairs are composed of dissimilar elements.

Heterozygous.—Having the allelomorphic pairs composed of dissimilar elements, resulting in the production of more than one kind of gametes.

Heterozygous Sex.—The sex in which the members of the chromosome pair that determines sex are unlike.

Homozygote.—A zygote resulting from the fusion of like gametes; an individual whose allelomorphic pairs are composed of similar elements.

Homozygous.—Having the allelomorphic pairs composed of similar elements, resulting in the production of only one kind of gametes.

Homozygous Sex.—The sex in which the members of the chromosome pair that determines sex are alike.

Hormone.—A substance secreted or found in some organ or tissue and carried in the blood to another organ or tissue which it stimulates to functional activity or the functions of which it inhibits.

Hybrid.—The progeny of a cross-fertilization between individuals belonging to different genotypes.

Impotence.—The inability to accomplish fertilization in any mating.

Inbreeding.—A system of mating in which the offspring have fewer ancestors than the maximum number possible.

Incompatibility.—The inability to accomplish fertilization in a particular mating.

Inheritance.—The material, living substances received by an individual from its parents.

Lethal.—Destructive of life.

Linkage.—The type of inheritance in which the factors tend to remain together in transmission from one generation to the next, owing to their location in the same chromosome.

Locus.—(*pl.* loci) A definite point or region in a chromosome at which is located a genetic factor or gene.

Mean.—The arithmetical average.

Median.—The point, on the scale used in arranging a frequency distribution, that divides the number of individuals into two halves.

Mode.—The class of greatest frequency.

Monoecious Plants.—Those having both sexes in separate flowers on the same individual.

Multiple Allelomorphs.—Factors occupying the same locus of homologous chromosomes; the characters conditioned by such factors.

Multiple Factors.—Two or more factors, all of which are needed to produce a certain result.

Mutant.—An individual having a different genotypic constitution from its parents, as the result of a change in the germplasm, and not of segregation, crossing-over, or irregular chromosome division.

Mutation.—The result of a change in genotypic constitution occurring independently of normal segregation, crossing-over, or irregular chromosome division; strictly, an alteration in the fundamental nature of the germplasm, usually in a single gene.

Non-disjunction.—The failure of the two members of a pair of homologous chromosomes to separate in cell division, with the result that both pass into one daughter cell and neither into the other.

Nucleus.—The more or less centrally located cell organ containing the chromatin.

Ontogeny.—The development of the individual, as distinguished from phylogeny.

Ovule.—The body that contains the egg of flowering plants and becomes the seed after fertilization and maturation.

Ovum.—(*pl.* ova) The egg.

Parthenogenesis.—The formation of an individual from an unfertilized germ cell.

Pedigree.—List of ancestors; genealogical tree.

Pedigree Culture.—A group of individuals whose pedigrees are known.

Pericarp.—In flowering plants, the seed covering, or ripened wall of the ovary.

Phenotype.—A group of individuals which are alike in appearances but which may differ germinally; the visible features, properties or functions of an individual; the sum of all the externally obvious characteristics which an individual possesses; contrasted with genotype.

Phylogeny.—The history of the evolution of a species or group, as distinguished from ontogeny.

Pistillate.—Producing functional ovules only.

Plastid.—A differentiated portion of the protoplasm within the cell, having the power of growth and reproduction by division and having a definite relation to certain physiological functions.

Population.—Any aggregation of individuals.

Prepotency.—Ability to impress individual characteristics upon offspring to a marked degree.

Protoplasm.—The living substance of cells.

Pure Line.—The descendants of a single individual that have not undergone any germinal change.

Recessive.—The opposite of dominant.

Reciprocal Hybrids.—The result of cross-fertilizations in which the parents are reversed as to sex.

Roguing.—The act of removing undesirable individuals from a varietal mixture by hand selection in the field.

Sex Chromosome.—The accessory chromosome which is associated with one or the other sex; one member of a pair of morphologically or physiologically distinct chromosomes which carry a factor or factors for sex.

Sex-limited.—A term applied to characters that are exhibited by one sex only.

Sex-linked.—A term applied to factors located in the sex-chromosomes or to the characters conditioned by them. Sex-linked characters may be exhibited by either sex.

Sex-ratio.—The relative proportion of males and females in a population.

Sexual Reproduction.—Reproduction resulting from the fusion of two germ cells.

Sire.—The male parent, used with reference to mammals; in contrast to dam, the female parent.

Soma.—The body, especially as distinguished from the germ or germplasm.

Somatic.—Pertaining to the body; contrasted with germinal, which means: " pertaining to the germ cells."

Somatoplasm.—The body tissues, as distinguished from reproductive tissues.

Species.—A group of varieties or a single variety which, in botanical characters and genetic relationship, can be differentiated from other groups or varieties belonging to the same genus or to other genera.

Sperm.—The male germ cell, spermatozoon (*pl.* spermatozoa).

Spore.—A one-celled or few-celled body which is separated from the parent for the purpose of reproduction.

Staminate.—Producing functional pollen only.

Sterility.—The lack of ability to produce normal living young; the opposite of fertility.

Stock.—A plant or part of a plant, usually a piece of the root, to which a cion is joined by grafting or budding.

Strain.—A group of individuals related by descent and differing in some respects from the other members of the variety.

Variety.—A group of individuals, within a species, which differ in some respects from the other members of the species.

Xenia.—The immediate, visible effect produced by pollen, usually resulting from double fertilization.

Zygote.—The result of the sexual fusion of two gametes; the individual that develops from the fertilized egg, usually containing the diploid number of chromosomes.

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